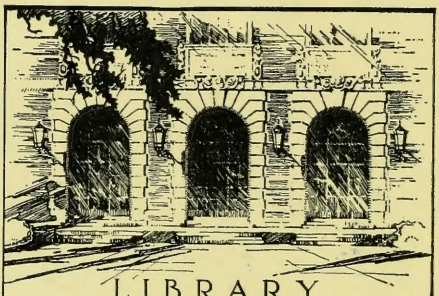

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A MONOGRAPH OF LEMNACEAE

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EDWIN HORACE DAUBS

ILLINOIS BIOLOGICAL MONOGRAPHS

34

THE UNIVERSITY OF ILLINOIS PRESS · URBANA · 1965

Board of Editors:
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THIS MONOGRAPH IS A CONTRIBUTION FROM THE DEPARTMENT OF BOTANY,
UNIVERSITY OF ILLINOIS. ISSUED DECEMBER, 1965

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Library of Congress Catalog Card No. 65–63594.

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ACKNOWLEDGMENTS

Sincere thanks are due to Dr. G. Neville Jones, Professor of Botany and Curator of the Herbarium, University of Illinois, under whose direction this investigation has been pursued; to Dr. Donald P. Rogers, Professor of Botany, University of Illinois, for valuable assistance in the preparation of the bibliography and for the Latin diagnosis; to Dr. William S. Hillman, Yale University, for providing living material of several species; to Professor P. Maheshwari, University of Delhi, for flowering specimens of *Wolffia microscopica;* to Mr. Jerry McClure, University of Texas, for his Landolt specimens; to Miss Gail Wisniewski, Miss Diana Heisler, and to my wife for the painstaking work of cataloging and checking specimens.

For the loan of specimens and other courtesies, I wish to express my appreciation to the curators of the following herbaria (abbreviations from Lanjouw and Stafleu, 1964):

MO	Missouri Botanical Garden
US	United States National Herbarium
F	Chicago Natural History Museum
UC	University of California
MICH	University of Michigan
FSU	Florida State University
ILL	University of Illinois

In addition some specimens have been examined from the herbarium of the Illinois State Natural History Survey (ILLS) and from the Jepson Herbarium (JEPS).

I. INTRODUCTION

The Lemnaceae are the simplest, and in the genus *Wolffia*, the smallest of the flowering plants. As such they interest and invite the serious study of botanists. Greater interest in the family has recently resulted from the demonstration of the value of certain species as experimental laboratory organisms. In addition, their economic importance as a link in the food chain of fishes and other aquatic animals has become increasingly recognized in the field of conservation. This renewed interest has served to draw attention to the fact that there is no recent taxonomic study of the family.

Although Linnaeus (1753) named four species in the genus *Lemna*, and added a fifth species in the same genus in his Mantissa Plantarum in 1766, the first actual monograph was that of Schleiden in 1839. In this work five species were recognized, in four genera, the same number but not the same genera recognized today. The monograph of Hegelmaier in 1868, plus a revision (or supplement) by the same author in 1896, constitute the only world-wide studies of the family. Thompson, in 1898, published a study of the species of North America, excluding Mexico. All other studies have been of a random nature or local in scope; no general or comprehensive work has been published during the twentieth century.

During this time two new species (genus *Spirodela*) have been recognized, three species of the genus *Wolffiella* have been reported in flower for the first time, and there is also a large number of new geographical records. It is clearly evident, therefore, that there is need for a critical review of the family in the light of this later knowledge, as well as some synthesis of the widely scattered data into a more readily available form. This study was prepared with these objectives in mind.

This monograph provides a key to the species based chiefly on the readily observable vegetative characters, detailed maps of the geographical distribution, descriptions of the flowers and fruits of those species whose flowers and fruits are known, and line drawings showing characters useful in identification. During this study over 4,000 collections, mostly consisting of more than one species, and each species represented by a great number of individuals, were examined. In addition, almost 200 collections, mostly including more than one species, were made by the author in various sections of the North American continent. These areas embraced the Great Lakes region including southern Canada, the Mississippi River valley including the Louisiana delta, Florida, Puerto Rico, and Mexico. All of these areas are particularly rich in species and populations of the Lemnaceae.

Seventeen species representing all four genera were included in these collections and many of these were maintained in living condition for considerable periods of time in the laboratory. No attempt was made to provide any special control of environmental conditions, such as light or temperature; thus the plants were observed under a variety of changing conditions. Considerable morphological and anatomical variations were observed, particularly in size and pigmentation and occasionally in the rootcap, and certainly more difficulty is encountered in correctly identifying such plants. However, identification can generally be readily made by following the keys presented herein, and the plasticity sometimes ascribed to the family seems to have been exaggerated.

The geographical distribution as shown on the maps and the morphological features included in the descriptions have been determined primarily from my own observations of living specimens or herbarium collections. The drawings are made from the composites of these observations rather than any single plant or collection. Credit has been given for any exceptions.

II. PHYLOGENY

The Lemnaceae have been universally placed in the order Arales, their relationship to the Araceae being traced through the water-lettuce, *Pistia stratiotes* L. The homologies of *Pistia* and *Spirodela polyrhiza* were set forth in some detail by Engler (1877) although Hegelmaier (1868) had earlier developed a similar concept of relationship. Engler interpreted the

region of the plant body ("frond" of most literature) above or in front of the basal pockets as foliar in nature, and the basal part of the plant as axial. He considered the buds in these pockets as equivalent to the lateral shoots of *Pistia,* although there are two such buds in *Spirodela,* one in each lateral pocket, and only one in *Pistia.* In each case the buds are lateral to the axis, not terminal. Hegelmaier, who had originally interpreted the frond as entirely axial, later (1896) modified his view to correspond to that of Engler. Another explanation, presented by Goebel (1921), interpreted the frond as being entirely foliar in nature. Engler's point of view seems to be the most nearly correct since it avoids the necessity for ascribing to leaves certain stem properties, and vice versa.

Arber (1920b) sought to answer two questions regarded as meriting more attention than Engler had given them. These were (a) the morphological nature of the pockets of *Spirodela* and their equivalent on the *Pistia* shoot, and (b) the region of the leaf represented by the "limb" of *Pistia* and the foliar area of the frond of *Spirodela.* On the latter question she interprets both of these as being of the nature of a petiolar phyllode and morphologically equivalent. The upper cover of the pockets is formed by a flattening and expansion of the axial region; the lower cover is formed by the vestigial remnants of the leaf sheath. Support for this theory is found in the small free flaps of the lower cover, which are homologized with reduced ligules. Thus the two pockets would be morphologically equivalent and also equivalent to the bud-containing pockets of *Pistia* formed in a similar manner.

Brooks (1940) agreed with Arber on the formation of the upper cover of the pouches but derived the lower cover from different sources. On the one side he interpreted it as being formed from the prophyllum or sheath which encloses the young growing point and which becomes stretched and fused, and on the other side as being formed from a bract, which in *Pistia* subtends the inflorescence. Thus these pockets would not be morphologically equivalent. Brooks supports this view further by pointing out that the bud of the new plant is borne in the axil of the prophyllum and the basal part (axis) of the frond, and that the flower is borne in the opposite pouch, subtended by the bract. Since this is the general nature of the growth habit of both *Spirodela* and *Lemna,* his hypothesis is an attractive one.

Disagreement with these conjectures of relationships has come from Lawalree (1945), who has presented arguments for the derivation of the Lemnaceae from the Naiadales through the Naiadaceae. These arguments include the similarity of habitat, certain similarities of flower development (true also for *Pistia*), and the homologizing of the flaplike structures on the pockets of *Spirodela,* the ligules of the Arber hypothesis, with the

"squamulae intravaginales" of the Helobiales. He also stated that the endosperm of *Lemna minor* was helobial in development. That this was not the case but rather that the endosperm was cellular from the beginning had been clearly shown by Brooks (1940), although Lawalree was doubtless unfamiliar with Brooks's work. More recently Maheshwari (1954, 1956a, 1956b), and Maheshwari and Khanna (1956), have fully confirmed Brooks's findings on *Lemna*, and have also found that the same condition holds true for *Wolffia* and *Arisaema*. These data tend to confirm the relationship of the Lemnaceae to the Araceae. A further weakness in Lawalree's position is his insistence that the sequence of change within the Lemnaceae be read as a progressive one, with *Wolffia* as primitive and *Spirodela* as advanced, a situation contrary to all present evolutionary concepts.

More recent work by Maheshwari (1958) tends, on embryological grounds, to place *S. polyrhiza* as the intermediate link between Araceae and Lemnaceae. In Araceae the development of the embryo sac is monosporic, whereas in those species of *Lemna* and *Wolffia* which have been studied, it is bisporic. In this study by Maheshwari, *S. polyrhiza* is shown to be monosporic, thus giving Lemnaceae a definite connecting link with the aroids.

Certain terminology which has been applied to the description of the flowers and flowering structures of Lemnaceae is more a tribute to their presumed ancestry than directly applicable to the nature of the structures themselves. The plants of Lemnaceae have been regarded as monoecious, and the flowers as unisexual and enclosed in a spathe, all terms more directly applicable to the Araceae. The spathe may well be a reduced perianth; the flower(s) might well be regarded as bisexual, consisting (in *Lemna*, for example) of a simple pistil and two stamens; there is no evidence of a spadix, and even the spathe is lacking in *Wolffia* and *Wolffiella*.

Most phylogenetic studies have considered chiefly the relationship of *Pistia* and *Spirodela*, so visibly similar that additional evidence merely further confirms an obvious relationship. The relationship of *Spirodela* to *Wolffia* is less apparent, and even with the intervening species of *Lemna* and *Wolffiella*, it is not possible to trace a direct lineal relationship. Additional evidence along this line is presented under the discussion of each genus.

Fossil Record

The fossil record of Lemnaceae is a meager one. The earliest records are from the Tertiary and at least one of these, *Spirodela scutata* (Dawson) Lesq., is not a member of the Lemnaceae but the genus *Nelumbo* of the

Nelumbonaceae. *Spirodela penicillata* (Lesq.) Cockerell is many-rooted but shows no veins in the plant body, and it seems questionable whether it should be placed in the genus *Spirodela,* although it is apparently Lemnaceae. It is present with an abundance of the fossil *Pistia corrugata* Lesq., not surprising in view of the similarity of habitat of the two species, although this association does not necessarily support the proposed relationship of the two families.

The Lemnaceae must have existed under conditions more favorable for fossil preservation than many plant forms more abundantly reported, and the lack of any extensive record is possibly a consequence of their being overlooked because of their small size, rather than any actual failure of preservation.

Chromosome Numbers

The infrequency of flowering and the lack of roots on two genera remove from consideration the two most common sources of material used in chromosome counts, i.e., spore mother cells and root tips. Blackburn (1933) gave the following counts: *Lemna minor* 40, *L. trisulca* 44, *L. gibba* 64, *Spirodela polyrhiza* 40, *Wolffia arrhiza* ca. 50. Brooks (1940) reports *L. minor* as having 42 chromosomes, and Lawalree (1943) reports *W. arrhiza* with ca. 40. Moore (Dore, 1957) reports *W. punctata* also with ca. 40. In this study chromosome counts were attempted only on the species of *Wolffiella* collected in living condition and on *Wolffia columbiana.* The meristematic tissue of young plants removed from the reproductive pouch was used in these efforts. In all cases the number appeared to be approximately 42, but the small nuclei and comparatively large number of chromosomes make accurate counts all but impossible. Neither these counts nor the other reports add any significant knowledge to the relationships within the family, although they tend to confirm the close relationship of *Wolffia* and *Wolffiella.*

III. SYSTEMATIC TREATMENT

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Lemnaceae Dumortier (1827) in Fl. Belg. 147; Agardh (1858) 46; Warming (1879) 154; Eichler (1875) 73; Bentham & Hooker (1883) 3: 1000; Prantl (1888) 242; Engler (1892) 78; Warming & Potter (1895) 307; Britton & Brown (1896) 1: 365; Britton (1901) 232; Small (1903) 229; Engler (1904) 92; Britton & Brown (1913) 1: 446; Wiegand (1914) 18; Rendle (1930) 267; Johnson (1931) 654; Willis (1931) 377; Small (1933) 248; Hutchinson (1934) 124; Wettstein

(1935) 1059; Engler & Diehls (1936) 152; Skottsberg (1940) 630; Jones (1950) 91; Lawrence (1951) 400; Jones & Fuller (1955) 119; Benson (1957) 347.
Lemnadeae S. F. Gray (1821) Nat. Arr. Brit. Pl. 2: 729.

Description of Lemnaceae

Small green aquatic plants, floating on or in the water, often forming a solid cover on the surface. Plants much reduced and simplified in structure, rootless or with few, nonfunctional, roots; vascular tissue lacking in many species. Reproducing chiefly by budding from a single basal pouch or two lateral pouches, many successive generations sometimes remaining attached by short stipes.

Most species flowering quite infrequently; plants monoecious, flowers unisexual, in some species surrounded or enclosed by a spathe. Flowers greatly reduced, pistillate flower solitary, style and stigma 1, simple; ovary unilocular, ovules 1–6, basal; staminate flowers solitary or 2, consisting of a single stamen, anther 1–2 celled, filament slender or fusiform, pollen scanty. Pollen grains uniformly 18–22 microns in diameter, spinulose, with a single germination pore. Giardelli (1935) has reported the pollen of *Wolffiella oblonga* as being only 11–15 microns in diameter; this would be a definite exception among the Lemnaceae to the rest of the family, as pollen diameter is one of the more constant characters throughout the family.

Fruit a utricle, seed large, smooth or ribbed, embryo straight, little or no endosperm; a prominent operculum, formed from the inner seed coat, at the micropylar end of seed.

Plants of definite tropical affinity and widespread in the temperate and tropical zones throughout the world. Some species overwinter in the temperate zones by means of specially produced dense dormant winter buds.

Family consisting of four well-defined genera including 28 species and one variety.

Key to Genera of Lemnaceae

1. Plants with 1 or more roots; 2 lateral reproductive pouches.
    2. Roots usually 2 or more on each plant, mature plants 5 mm. or more in length. ..... SPIRODELA
    2′. Roots solitary on each plant, plants usually less than 5 mm. in length. ..... LEMNA

1′. Plants rootless; each with a single basal reproductive pouch.
    3. Fronds flat, thin, ligulate, appearing two-dimensional. ..... WOLFFIELLA
    3′. Fronds ellipsoid to globose, more or less isodiametric, obviously three-dimensional. ..... WOLFFIA

Description of Genus *Spirodela*

Spirodela Schleiden in Linnaea 13: 391. 1839.

Plants floating on the surface of the water, 3–5 or more remaining connected often by elongated stipes; individuals measuring from 3.0–10.0 mm. long, from 1.2–8.0 mm. wide, infrequently exceptional plants exceeding these measurements; orbicular, obovate, or slightly reniform in outline, slightly to extremely asymmetrical; each plant with 2–18 roots, fascicled, each root with a vascular strand throughout its length; 3–15 nerves, obscure or prominent; rootcap sharp-pointed, acuminate to mucronate; all species abundantly red-purple pigmented on one or both surfaces, the epidermis also containing more or less abundant brown pigment cells resulting in a punctate appearance, especially in the dead or cleared plants; aerenchymatous tissue throughout the plant body, the air spaces sometimes greatly inflated.

Flowers unisexual, 2 (rarely 3) staminate, and 1 pistillate, borne in 1 of the 2 lateral reproductive pouches, enclosed in a spathe; ovary with 1–4 ovules, these amphitropous to anatropous; fruit slightly winged, broadly elliptical; seed longitudinally ribbed and transversely striate or smooth with spongy outer layer. All species rich in raphides and druses.

Five species of this genus are here recognized and one variety is described for the first time. One species, *S. polyrhiza*, is of cosmopolitan distribution; the others are of more limited occurrence.

No one has seriously questioned the generic status of *Spirodela* since its establishment by Schleiden, although Hutchinson (1934) considered it a subgenus of *Lemna*. Hegelmaier (1868, 1896) placed *Spirodela* and *Lemna* together in the tribe Lemneae; Lawalree (1945) placed them together in a subfamily Lemnoideae. The close relationship of the two genera is shown by either system; yet their separate generic status is well justified. The greater size and complexity of the plant body of *Spirodela*, including its increased vascularization, larger number of roots, tendency toward a plural number of ovules, and the monosporic development of the embryo sac (in *S. polyrhiza*) all combine to differentiate this genus from others in the family.

Flowering is generally rare in *Spirodela*, and the only species with wide distribution, *S. polyrhiza*, is characterized by the production of a densely cellular, compact bud, or turion, by which means it successfully overwinters in adverse climates. *Spirodela* may be regarded as the ancestral genus of the family, with the trend being one of continuing reduction and simplification.

Key to Species and Varieties of *Spirodela*

1. Plants larger (up to 10 mm. in diameter), orbicular to obovate, with many roots.

2. Fronds flattened on both surfaces, nerves prominent; not inflated.
    3. Prophyllum penetrated by only the first primary root, plants producing turions. . . . . *S. polyrhiza*
    3′. Prophyllum penetrated by first 2 primary roots, plants not producing turions. . . . . *S. biperforata*
2′. Fronds strongly convex beneath with noticeably inflated air spaces.
    4. Prophyllum penetrated by first 3–4 primary roots, plants not producing turions. . . . . *S. intermedia*
    4′. Prophyllum penetrated by only the first primary root, plants producing turions. . . . . *S. polyrhiza* var. *masonii*

1′. Plants smaller (less than 5 mm. in diameter), elongate-obovate to slightly reniform, with few (2–4) roots.
    5. Fronds abundantly punctate, biconvex, infrequently only 1 root, usually 2–3 roots. . . . . *S. punctata*
    5′. Fronds less noticeably punctate, at least while living, ventral surface convex, 2–5 roots. . . . . *S. oligorhiza*

1. SPIRODELA INTERMEDIA W. Koch

Plate 2

Spirodela intermedia W. Koch in Ber. schweiz. bot. Ges. 41: 114. 1932.

Plants floating, commonly 3–5 cohering; individuals 5.0–10.0 mm. long, 4.0–8.0 mm. wide, and up to 3.0 mm. thick as a result of the inflated condition and resulting convexity of the ventral surface; in outline, orbicular to elliptic, asymmetrical; dorsal surface flat, both surfaces highly pigmented; 7–10 nerves weakly perceptible; roots 10–18 or more, exceeding in number those of *S. polyrhiza;* rootcap acuminate; brown pigment cells in moderate number in epidermis, fruit, style, and stigma.

Flowers characteristic of the genus; fruit winged, usually four-seeded, ovules anatropous; seed ribbed. Raphides and druses abundant throughout plant.

Type locality: Uruguay: Montevideo.

Type collection: Arechavaleta 2502 in Inst. Bot. E. T. H., Turici, Zurich. Also cited at the same time, Herter 629 (F, UC, MICH); these specimens examined.

Distribution: Argentina, Brazil, Colombia, Uruguay, Venezuela; Panama.

Collections examined: ARGENTINA: Peterson 2813 (MO), Venturi 9452 (US), Giardelli 502 (UC), Burkhart 8521 (UC); BRAZIL: Smith & Klein 11254 (US); COLOMBIA: Mason 13750 (UC), Zainum, Molina & Barkley 19 Bo 079 (US), Fassett 25363 (US); URUGUAY: Gilbert 1337 (US), Venturi 6432 (US), Herter 629 (F, UC, MICH), Lorentz (F);

VENEZUELA: Lasser 2004 (MICH); PANAMA: Bartlett & Lasser 16981, 16824a (MICH).

This species has the most complex plant body of any of the duckweeds. It combines the inflated air spaces and multiseeded fruits present in *Lemna gibba* with the multiple roots and increased vascularization present in *S. polyrhiza.* Thus, to some extent it fulfills Brooks's (1940) requirements for the ancestral type of the family. Although apparently unfamiliar with this species, he postulated some of its characteristics in a proposed phylogeny of the family.

The authority for the binomial, Walo Koch, first described the species from herbarium material, after he found some of the plants adhering to other water plants which he was studying. Later (1933) he added to his description when living plants were found. *S. intermedia* has since been reported from locations as shown in the collections examined, most of these having been made since Koch's original report. Giardelli (1939a) reports that all material she has examined from Argentina which is usually labeled *S. polyrhiza* is actually *S. intermedia,* and that the former species should be dropped from treatments of the flora of that country. This statement apparently may be expanded to include all of the South American flora.

Certainly this is one of the most interesting morphologically of any of the duckweeds, and its wide distribution in South America and its occurrence in Panama, although apparently infrequent in all areas, tends to support Brooks's hypothesis that it is an ancestral type.

2. SPIRODELA POLYRHIZA (L.) Schleiden

Plate 3

Lemna polyrhiza L. in Sp. Pl. 970. 1753.
Lemna polyrhiza Lam. in Fl. Fr. 2: 189. 1778.
Lenticula polyrhiza Lam. *loc. cit.*
Lemna orbiculata Roxb. in Hort. Beng. 66. 1814; Fl. Ind. 3: 565. 1832.
Lemna orbicularis Kit. ex Schultes in Oestr. Fl. 2nd ed. 1: 64. 1814.
Lemna thermalis Beauv. ex Nutt. in Gen. Amer. 1: 19. 1818.
Spirodela polyrhiza (L.) Schleid. in Linnaea 13: 392. 1839.
Lemna bannatica Waldst. & Kit. ex Schleid. *loc. cit.*
Telmatophace polyrhiza Godr. in Fl. Lorr. 1st ed. 3:18. 1843; 2nd ed. 2: 327. 1857.
Lemna major Griff. in Notul. 3: 216. 1851.
Telmatophace orbicularis Schur in Verh. siebenb. Ver. Naturw. 4: 70. 1853.
Lemna transsylvanica Schur in Enum. Pl. Transs. 635. 1866.
Lemna umbonata A. Br. ex Hegelm. in Lemnac. 146. 1868.
Spirodela atropurpurea Montand. in Guide Bot. 309. 1868.
Lemna maxima Blatter & Hallb. in Jour. Ind. Bot. 2: 49. 1921.
Spirodela maxima (Blatter & Hallb.) McCann in Jour. Bombay Nat. Hist. Soc 43: 158. 1942.

Plants floating, usually 2–5 remaining connected by elongate peltately attached stipes; individuals from 3.0–10.0 mm. (commonly 5.0–8.0) long, 2.5–8.0 mm. wide; orbicular to obovate, slightly asymmetrical; dorsal surface flat, yellow-green in color, the nodal area often dark and prominent; the lower surface flat to slightly convex, usually purplish to red; 5–15 prominent nerves, each with a single vascular strand; roots 5–12, fascicled, each with a single vascular strand; rootcap long, thin, acute, often slightly curved.

Flowers characteristic of the genus, except rarely 3 staminate flowers; spathe open only at the top; anthers and stigma sparsely punctate with brown pigment cells; ovary with 1 amphitropous ovule or 2 anatropous ovules; fruit slightly winged; seed slightly compressed, smooth or minutely reticulate.

Forming turions at all seasons but abundantly so in the fall.

Type locality: Europe.

Type collection: None listed in Savage (1945).

Distribution: Cosmopolitan, being found to some extent throughout most temperate and tropical regions of the world, except of limited distribution in Africa, and apparently lacking in South America.

Collections examined: UNITED STATES: ARKANSAS: Engelmann (MO), Daubs 825, 826, 834, 848, (ILL); CALIFORNIA: Palmer 327 (F), Mason 14561, 14630 (FSU), Drouet & Richards 4218 (F); CONNECTICUT: Eames (US), Eaton (MO); DELAWARE: Canby (F), Cummins (MO); FLORIDA: Godfrey 57712, 54467 (FSU), Daubs 661, 667, 662, 740 (ILL), Curtiss 4544 (F, MO); GEORGIA: Thorne 7346 (MO), Thorne 4056 (F); HAWAII: Degener 8933 (MICH, MO); IDAHO: Offerd & Eppling 8254 (F, MO); ILLINOIS: V. H. Chase 6169 (ILL), G. N. Jones 17380, 22255 (ILL), A. Chase (ILL), Daubs 803, 863, 860 (ILL); INDIANA: A. Chase 1986 (ILL), King 255 (F), Standley 57477 (F), Greenman 2154 (MO); IOWA: G. N. Jones 22323 (ILL), Fink 398 (US), Thorne 10740 (UC), Hayden 10135, 10136 (MO); KANSAS: Norton 533 (MO); KENTUCKY: McFarland 47 (MO), Alexander 289, 332a (US); LOUISIANA: Ball 586 (US), Reese 5809 (FSU), Daubs 792, 916 (ILL), Palmer 8923 (MO); MAINE: Steinmetz 324 (ILL); MARYLAND: Killip 36669 (MO); MASSACHUSETTS: Smith & Harris 827 (MO, MICH), Seymour 458 (MO); MICHIGAN: Gillman (ILL, MO), Palmer 40468a (MO), Burgess 94 (F); MINNESOTA: Moore & Huff 18469 (ILL), Moyle 560 (F), Metcalf 1803 (US); MISSISSIPPI: Daubs 798, 797, 796 (ILL); MONTANA: Kramer & Barkley 1902 (US), Whitford 315 (F); MISSOURI: Steyermark 20690 (F), Palmer 56307 (F), Trelease 8120 (MO), Bush (MO), Thompson (MO); NEBRASKA: Tolstead (MO), Bates 1132, 1137, 1139 (MO); NEW JERSEY: Adams 290 (MO), Martindale (MO), Austin 8056 (MO); NEW

YORK: Killip 12494 (US), Leggett (MO), Muenscher & Maguire 2114, 1039 (MO); NORTH CAROLINA: Kearney (US); NORTH DAKOTA: Stevens 2019 (UC), Stevens 282 (F); OHIO: Hicks (MO); OKLAHOMA: Stevens 690 (MO); OREGON: Hall (MO), Waite (US), Lawrence 1677 (US); PENNSYLVANIA: Fergus (F); RHODE ISLAND: Congdon (MO); SOUTH CAROLINA: Godfrey & Tryon 721 (MO), Ravenel (MO); TEXAS: Ferguson & Long (F), Bush 1439 (MO), Tharp (MO), Daubs 855 (ILL); UTAH: M. E. Jones 5979 (US), Maguire 3272 (MO); VERMONT: Dutton (MICH, MO), Mathias 260 (MO); VIRGINIA: Fernald & Long 8180 (MO), Shull 242 (MO); WASHINGTON: Suksdorf 2819 (MO, US, F); WEST VIRGINIA: Berkley 1462 (MO); WISCONSIN: Bebb 1519 (F), Hale (MO), Fassett 17419 (MO).

CANADA: BRITISH COLUMBIA: Calder 10898 (UC), Macoun 88277 (US), Macoun 28103 (MO); ONTARIO: Daubs 504, 506 (ILL), Calder 631 (MO), Fowler (MO, F); QUEBEC: Marie-Victorin 43–523 (UC), Churchill (MO).

MEXICO: Wiggins 6416 (MICH), Matuda 19719 (UC), Daubs 634, 616 (ILL), Pringle 5384 (UC, F), Steere 1567 (MICH).

CENTRAL AMERICA: EL SALVADOR: Fassett 28641, 28542, 28685, (F), Fassett 28567 (F, MO); GUATEMALA: Smith 1963 (US), Cook & Martin 138 (US), Steyermark 31831, 34532, 30172 (F); HONDURAS Standley 17703, 56860, 18093 (F).

WEST INDIES: CUBA: Wright 66 (MO); DOMINICAN REPUBLIC: Fuertes 1161 (US, MO, F); HAITI: Leonard 10076 (UC), Leonard 3548 (US), Bartlett 17468 (MICH); JAMAICA: Britton 3025 (MO), Harris & Britton 10510 (US); PUERTO RICO: Britton & Shafer 1795 (MO, F), Britton 5805 (US).

EUROPE: AUSTRIA: Kerk (MO); BALKANS: Nyarady 131 (MO, US); BELGIUM: Haesendouck (F); FINLAND: W. Laurent & Hjelt (MO), Lindberg 144, 554 (MO, UC), Johanssen (MO); FRANCE: Jeanpert (F), Tidestrom 13155 (F, UC), Copineau (US), Corbiere (US); GERMANY: Kurth (F), Engelmann (MO); HUNGARY: Tscherning 4775 (F), Dorfler 3893 (MO); ITALY: Borza 1316 (MO); NETHERLANDS: Boetje & Van Ruyven (F); POLAND: Krawiec 299 (MO); SCANDINAVIA: Samuelson (MO), Moller (MO), Asplund (MO); SIBERIA: Maak (F), Mameev 699 (US); SWITZERLAND: Brossier (UC).

ASIA & PACIFIC: CHINA: Tsu 126 (US), Bonati 2870 (UC), Maire 2870 (MICH); INDIA: Koelz 18648 (MICH), Stewart 1066 (UC), Stewart 3337 (MO), Koelz 4917 (MICH, UC), Thivy 125 (MICH); JAPAN: in 1887 (US); PHILIPPINES: Merrill 4244 (US), Van Overberg 3319 (F); NEW GUINEA: Clemens 41513 (MICH).

Spirodela polyrhiza is rather easily identified and only infrequently confused with other members of the genus, although the two South

American species, *S. biperforata* and *S. intermedia*, were identified under the older binomial until Walo Koch (1932, 1933) published his diagnoses. In *S. polyrhiza* only the first, or oldest root, penetrates the prophyllum of the young plant whereas in *S. biperforata*, as the name implies, the first two roots do so. *S. intermedia* is readily distinguished from *S. polyrhiza* through its inflated, gibbous air spaces. The tropical forms of *S. polyrhiza* differ somewhat from the temperate forms in being slightly thicker and with less prominent nerves, but otherwise partake of the species characteristics.

S. polyrhiza flowers as rarely as any member of Lemnaceae, and is the only species of the genus known to produce turions.

2a. SPIRODELA POLYRHIZA var. MASONII var. nov.

Type locality: Holland: Edam.

Type collection: Mason 14846 (UC).

Frons natans, elliptico-rotundata, nervis facile perceptabilibus; dorso subplano, ventro valde convexo fortiter inflato. *S. polyrhizae* (L.) Schleiden valde affinis. Radices usque ad 10, solum prima folium rudimentale perforans, calyptris acutis.

Resembling the species in most characteristics, this variety differs from *S. polyrhiza* in being decidedly inflated and gibbous on the ventral surface, in this respect being similar to *S. intermedia* or *L. gibba*. Its relationship to the parent species is shown from the fact that it produces turions abundantly, and that only the first, or oldest root, pierces the prophyllum of the young plant. It is known only from the Netherlands from the following collections: Florschutz, Sept. 25, 1948 (MO); Mason 14846, Sept. 1, 1954 (UC); Dr. G. deChalmot (US).

3. SPIRODELA BIPERFORATA W. Koch

Plate 5

Spirodela biperforata W. Koch in Ber. schweiz. bot. Ges. 42: 188. 1933.

Plants floating, up to 5 cohering; 5.0–6.5 mm. long, 3.5–5.0 mm. wide; elongate-elliptical, strongly asymmetrical; nerves 10–12 clearly visible; fronds generally flat on both surfaces, medium thick, but not inflated, moderately red-purple pigmented; roots 5–10, rootcap acute, the first 2 primary roots penetrating the prophyllum.

Flowers typical of the genus, spathe open only by a slit at the top; pigment cells in anther, filament, and stigma; ovules 2, anatropous; immature fruit ovoid, mature fruit unknown.

Type locality: Surinam (Dutch Giana): Paramaribo.

Type collection: G. H. Bunzli in 1932, type in herbarium of Inst. Bot. E. T. H., Turici, Zurich.

Distribution: Argentina, Colombia, Peru, Surinam, Venezuela; Cuba, El Salvador.

Collections examined: ARGENTINA: Gruner (UC), Jorgensen 3373 (MO); COLOMBIA: Amortegi 417 (US), Hermann 11315 (MICH), Viereck (US), Molina & Barkley 19 Bo 206 (US); VENEZUELA: Salazar 7 (US); CUBA: Walker, in June 1946 (MICH); PERU: Killip & Smith 27706 (US); EL SALVADOR: Fassett 28576 (US).

This species is similar to *S. polyrhiza*, and for some time I was inclined to regard it merely as a variety of this latter species. However, with the finding of the Walker and Salazar collections, previously not identified, and clearly to be associated with Koch's description, I have recognized his species as valid.

4. SPIRODELA OLIGORHIZA (Kurz) Hegelmaier

Plate 4

Lemna gibba sensu Blanco in Fl. Filip. 1st ed. 672. 1837.
Lemna oligorhiza Kurz in Jour. Linn. Soc. London 9: 267. 1867.
Lemna melanorhiza F. Muell. ex Kurz in Jour. Bot. 5: 115. 1867.
Lemna pleiorhiza F. Muell. ex Kurz *loc. cit.*
Spirodela oligorhiza (Kurz) Hegelm. in Die Lemnaceen 147. 1868.
Lemna javanica Bauer ex Hegelm. *loc. cit.*
Lemna pusilla Hegelm. *loc. cit.*

Plants floating on the water, usually 2–5 attached; single plants 2.5–5.0 mm. long, 1.2–3.0 mm. wide; elliptical-obovate to slightly reniform, base elongate acute, asymmetrical; dorsal surface yellow-green, flat to convex; ventral surface convex, frequently somewhat inflated; obscurely 3–5 nerved; roots 2–5, root tip straight, rootcap mucronate; plants usually strongly red-purple pigmented below, occasionally so above, also moderately punctate with brown pigment cells.

Flowers typical of the genus, spathe open along one side; fruit ovoid, slightly winged, one-seeded; ovule amphitropous; seed ribbed, reticulate, operculum prominent. Flowering frequently.

Raphides and druses abundant throughout.

Type locality: India: Calcutta.

Type collection: Kurz, described by Hegelmaier.

Distribution: Reported rarely from India, China, Australia, Fiji Islands, New Caledonia; now possibly more prevalent in the United States.

Collections examined: UNITED STATES: FLORIDA: Daubs 757, 651, 671, 666, 670, 672, 673, (ILL), Godfrey 5768a, 60541, (FSU), Godfrey and Reinert 60596, 60574, (FSU); ILLINOIS: Daubs 545, 803, (ILL); LOUISIANA: Daubs 780, 782, 786, 916, 915, (ILL); MISSOURI: Saeger (US); CALIFORNIA: Heckard and Bacigalupi 7693, (JEPS); AUSTRALIA: Bailey 183 (US), Helms 411, (UC), Boorman (US); CHINA:

Barchet (US), Norton 1227, (US); FIJI ISLANDS: Wilkes Exp. (US), Seeman 656, 657, (MO); NEW CALEDONIA: Balaura 3771, (MO), Balaura 3111, (UC), Bonati (UC), Franc (MICH).

Spirodela oligorhiza has the smallest plants of the genus except for the rarely reported *S. punctata*, and is more likely to be confused with *Lemna* species than with its congeners. It is readily identified by its multiple roots, brown punctation, and generally biconvex surfaces. It is variable in many features, including size and convexity, but these seem not consistent enough to justify the many varietal epithets which are here placed in synonymy. This species is readily maintained in culture; it is often used as an aquarium plant; and therefore it is easy to make repeated observations on clonal cultures.

The distribution pattern is an interesting one (see Daubs, 1962). Originally reported from India and regarded as a Far Eastern species, it has been introduced into the United States, apparently as an aquarium plant, and is now rather widespread. It has been reported from California, Illinois, Louisiana, and Florida.

Although exact dates of publication are unavailable, the priority of publication of the binomial *Lemna oligorhiza* by Kurz in the *Journal of the Linnean Society* is clearly established by the author through his subsequent reference to this publication in an article in the *Journal of Botany* of the same year, 1867.

5. SPIRODELA PUNCTATA (G. F. W. Meyer) Thompson

(not illus.)

Lemna punctata (G. F. W. Mey.) in Prim. Fl. Esseq. 262. 1818.

Spirodela punctata (G. F. W. Mey.) Thomp. in Rep. Mo. Bot. Gard. 9: 28. 1898.

Plants solitary or cohering in groups of 3–5; 2.0–3.5 mm. long, 1.2–2.0 mm. wide; elliptical to slightly reniform, base elongate, asymmetrical; biconvex, not inflated; obscurely three-nerved; roots 1–3; rootcap long, thin, mucronate; intensely punctate on both surfaces with brown pigment cells.

Flowers typical of the genus; spathe open only at top; fruit lenticular, winged, one-seeded; ovule amphitropous.

Type locality: British Guiana: Essequibo River.

Type collection: Unknown, description by Thompson from specimens cited, these examined, and the only collections known: Wilkes Expedition, Tierra del Fuego, 1839 (MO, US).

There can be no doubt about the close relationship of this species to *S. oligorhiza*. The specimens from which Meyer made his original descriptions were apparently lost and never examined by anyone else, and both Schleiden and Hegelmaier dismissed Meyer's specific epithet with bare

mention. Thompson (*loc. cit.*) in describing the collection of plants from the Wilkes Expedition felt that they fitted Meyer's description so well that he applied Meyer's specific epithet, transferring it to the genus *Spirodela.*

The large number of plants with but a single root, the intensely punctate condition, and small size help to distinguish the species from *S. oligorhiza.* Since the only collection was made more than a century ago, the species may have become extinct.

Description of Genus *Lemna*

Lemna Linnaeus in Gen. Pl. Ed. 5. 417. 1754.
Lemna Linnaeus in Sp. Pl.: 970. 1753.
Lenticula Mich. ex Adans. in Fam. 2: 471. 1763.
Hydrophace Haller in Hist. Stirp. Helv. 3: 68. 1768.
Telmatophace Schleid. in Linnaea 13: 391. 1839.
Staurogeton Reichb. in Nom. 33. 1841.

Plants free-floating upon or beneath the surface of the water; solitary, or many remaining attached; mostly orbicular to obovate in outline, much elongated in *L. trisulca;* symmetrical to asymmetrical; some species strongly red-purple pigmented; all species with a single root peltately attached; most with a single nerve and some with additional lateral nerves; two lateral pouches, one on either side of the stipe near the base, young fronds or flowers or both being borne in these. Plants small, seldom exceeding 5 mm. in length, except in *L. trisulca.*

Plants monoecious, 2 staminate and 1 pistillate flower, all enclosed in a membranous spathe, this open along one side or nearly closed with only a slit at the top; ovary one-celled, one or more ovules, orthotropous, amphitropous, or anatropous; style circular, hollow; stigma concave, with a mucilaginous droplet at maturity; filament slender, anthers two-celled, didymous, transversely dehiscent; staminate flowers maturing at different times.

Fruit a 1–6 seeded utricle; seeds typically ribbed with transverse striations, operculum prominent.

Key to Species of *Lemna*

1. Fronds usually submerged, long-stipitate, many remaining attached, forming long chains. . . . . *L. trisulca*
1′. Fronds usually floating, short-stipitate or sessile, characteristically 2–5 attached.
    2. Dorsal surface flat, smooth, with no prominent protuberances; one-veined or veinless.
        3. Plants narrowly elliptical, often 8–10 attached; base asymmetrical. . . . . *V. valdiviana*

3′. Plants smaller, oval, symmetrical, seldom more than 2 remaining attached. ..... *L. minima*

2′. Dorsal surface with more or less prominent protuberances, indistinctly to prominently three-veined.

4. Root sheath with definite wings or appendages.

5. Fronds distinctly three-nerved, flat, thin. ..... *L. trinervis*

5′. Fronds not prominently nerved, generally biconvex, apical papilla prominent. *L. perpusilla*

4′. Root sheath without wings or appendages.

6. Ventral surface of frond flat to slightly convex but not inflated.

7. Dorsal surface dark green, frond apex symmetrical, air spaces not prominent. ..... *L. minor*

7′. Dorsal surface mottled yellow-green, apex asymmetrical, air spaces prominent. ..... *L. gibba*

6′. Ventral surface of frond noticeably convex, the air spaces inflated; both surfaces showing red-purple coloring.

8. Air spaces strongly inflated, gibbous; apex asymmetrical, fruit winged. ..... *L. gibba*

8′. Air spaces slightly inflated, apex symmetrical, plants smaller, fruit not winged.

9. Fruit two-seeded. ..... *L. disperma*

9′. Fruit one-seeded. ..... *L. obscura*

6. LEMNA GIBBA Linnaeus

Plate 8

Lemna gibba L. in Sp. Pl. 970. 1753.
Lenticula gibba Moench in Meth. 319. 1794.
Lenticula gibbosa Renault in Fl. Dep. Orne. 40. 1804.
Telmatophace gibba Schleid. in Linnaea 13: 391. 1839.
Lemna tricorrhiza Thuill. ex Schleid. *loc. cit.*
Telmatophace arrhiza Schur in Verh. siebenb. Ver. Naturw. 4: 70. 1853.
Telmatophace gibbosa Montand. in Guide Bot. 308. 1868.

Plants solitary or commonly 2–4 cohering; 3.5–6.0 mm. long, 2.5–5.0 mm. wide; orbicular to obovate, apex asymmetrical, base symmetri-

cal, subacute; upper surface flat to slightly convex, lower surface flat to convex or strongly inflated and then globose; nerves 3–5, indistinct; root sheath short, cylindrical, prominent; rootcap straight, usually obtuse but sometimes acute; air spaces large, irregular, in two or more layers, frequently inflated; fronds mottled yellow-green on upper surface, frequently strongly red-purple pigmented on both surfaces.

Flowers typical of the genus; fruit broadly cordate to obovate, winged, 1–6 seeded, more commonly 1–3 seeds; ovules amphitropous if only one, anatropous if more than one; seed ribbed with prominent operculum and hilum, these strongly red-purple colored.

Type locality: Europe.

Type collection: None listed in Savage (1945).

Distribution: Rather widely distributed throughout temperate and tropical regions of the world, although of apparently limited occurrence in Africa, and until reported here, regarded as absent from the eastern United States.

Collections examined: UNITED STATES: ARIZONA: Gould, Fletcher & Anderson 5250 (UC), Thornber 5273 (MICH), Wiggins 8501 (US), Wiggins 8202 (MO); CALIFORNIA: Heller & Brown 5571 (MO, MICH, US, F), Jepson (MO), Torrey 504 (US), Nobs & Smith 1538 (UC), 1222 (ILL), Smith & Nobs 1826 (UC), Wiggins 3307 (UC), C. H. Thompson, several in 1902 (MO), Carter 345 (ILL), Abrams 3983 (MO); COLORADO: Gooding 1788 (MO); FLORIDA: Godfrey 54666 (FSU); IDAHO: Leiburg 1596 (MO), Merrill 389 (US), Trelease & Saunders 3187 (MO), Nelson & Macbride 1611 (MO); ILLINOIS: Daubs 877 (ILL), Burrill in 1894 (ILL); MINNESOTA: Moyle 2321 (UC); MISSISSIPPI: Daubs 798 (ILL); MONTANA: Harz (MO), Maguire 628 (UC); NEVADA: Kennedy 4258 (MO), Archer 5713 (UC); NEW MEXICO: Fosberg 3888 (UC), Wooten (US); NORTH DAKOTA: Waldron & Manns (US); OREGON: Ownby 1798 (ILL, MO); TEXAS: Palmer 11398 (US, UC, MO); UTAH: Mulford 373 (MO), M. E. Jones 5321 (US); WYOMING: A. Nelson (ILL, MO), A. Nelson 9590 (MO), Porter 6570, 6630, 5748 (UC).

MEXICO: DISTRITO FEDERAL: Daubs 605 (ILL), Fassett 28430 (MO, F, MICH), Hahn; PUEBLA: Daubs 608 (ILL), Fassett 28479 (F, US), Arsene 1063 (MO, ILL, US); MICHOACAN: Daubs 615, 616, 621 (ILL); SONORA: Hartman 990 (MO, F, US), Rose, Standley, & Russell 12458 (US), Rose, Painter & Rose 9852 (US); BAJA CALIFORNIA: Wiggins & Gillespie 3967 (F); CHIHUAHUA: Rose & Hough 4942 (US).

HAITI: Eyerdam 344 (MO).

SOUTH AMERICA: ARGENTINA: Eyerdam & Beetle 22854 (MO, UC), Hieronymus 489 (US), Giardelli 521, 565 (UC); BOLIVIA: Julio II–44, II–196 (US); COLOMBIA: Triana 682 (MO); CHILE: Hastings 597 (UC), Rose 19373 (US); ECUADOR: Spruce 5064 (MO); PERU:

Eyerdam 9081 (UC), Herrera, in 1928 (F); SURINAM: Weigelt, in 1827 (MO); URUGUAY: Herter 16 (MO, UC), Herter 681 (MO).

INDIA: Koelz 1625 (MICH), Stewart 13825 (MO, US, UC), Stewart 3379 (MO, UC), Stewart 12132 (MO).

CHINA: Niao 9077 (F); OUTER MONGOLIA: Chaney 319 (UC).

PHILIPPINES: Merrill, in 1914 (MO).

AFRICA: SOUTH AFRICA: Drege (MO), Eiglon 456 (MO); KENYA: Verdcourt 718B (MO); ERITREA: Pappi 5055 (UC); NATAL: Schlechter 5757 (US); CONGO: Van Laesengonck, in 1875 (F).

EUROPE: AUSTRIA: Kerk, in 1875 (MO, F), Dorfler (MO); ENGLAND: Pease 9941 (F), Lomax 4 (US), Moggridge (US); FRANCE: Copineau (US), Jeanpert (F), Trappes (F); FINLAND: Johanssen 533 (MO, UC), Cedercrentz 1101 (MO, UC), Lindberg 1100 (MO); CZECHOSLOVAKIA: Suza, in 1928 (MO); GERMANY: A. Braun, in 1868 (MO), no collector given but bearing Hegelmaier's annotation, near Mannheim (MO); PORTUGAL: Gay (US); SWITZERLAND: Bossier (UC); NETHERLANDS: Florschutz & Kramer (MO); POLAND: Krawiec (MO), Gandoger (MO); ITALY: Rabenhorst (MO), Gussome (MO); SPAIN: Pitard 684 (MO), Bornmuller 2869 (MO), Trelease (MO), Barbey 986 (US).

The gibbous or inflated form of *L. gibba* is easily recognized, and while there is some obvious variation in the degree of gibbosity, there is not a continuous gradation between the gibbous and the flatter forms. Even the very young fronds of the gibbous forms show this characteristic to a marked degree. Most of the intermediate forms (noticeably convex below and with prominent air spaces) probably belong to either *L. obscura* or *L. disperma,* both of which are always smaller than *L. gibba,* and also convex on the upper surface. The flat form has been described (Guppy, 1894) as an overwintering form but it seems doubtful if this is its exclusive function, since it also grows, reproduces, and apparently fruits normally. Mason (1957) reports the flat form as fruiting infrequently, but I have not seen any fruits of this form. The gibbous form flowers and fruits with some regularity, apparently behaving as a typical long-day plant (Hillman, 1961b). The differentiation of plants of this species from those of *L. minor* is discussed under the latter species.

7. LEMNA DISPERMA Hegelmaier

Plate 12

Lemna disperma Hegelm. in Bot. Zeit. 154. 1871.
Lemna disperma var. *fallax* Hegelm. Bot. Jb. 21: 1896.
Lemna parodiana Giardelli in Notas Mus. La Plata 2: 12. 1937.

This species partakes of the essential features of *L. obscura* as described in this treatise, differing only in number of seeds (two, as described by

Hegelmaier), and in having an acute rootcap. Even on this character, Hegelmaier (1896) describes a variety, var. *fallax*, which has an obtuse rootcap. In his original description (*loc. cit.*) Hegelmaier says that he had originally classified *L. disperma* as *L. gibba*, but that upon finding only two-seeded forms he felt that this and other differences merited the establishment of the new species. This also resulted in his removing the species *L. gibba* from the flora of Australia. That these two species, as well as *L. obscura*, are closely allied, seems obvious from a comparison of their descriptions. (See discussion of *L. obscura*.)

Type locality: West Australia: Swan River, Upper Blackwood River, and Lake Lefroy, all cited by Hegelmaier.

Type collections: Drummond, Cronin, and F. Muller, all cited by Hegelmaier.

Distribution: Australia, New Zealand, Tasmania (Hegelmaier); Argentina (Giardelli), Peru (Wilkes Expedition).

Collections examined: Giardelli 503, 535 (UC), Wilkes Expedition (US). This latter collection identified as *L. parodiana* by Giardelli and *L. gibba* by C. H. Thompson.

8. LEMNA OBSCURA (Austin) comb. nov.

Plate 12

Lemna obscura (Austin) comb. nov.
Lemna minor var. *obscura* Austin in A. Gray Man. Bot. 5th ed. 479. 1867.
Lemna minor var. *colorata* Hegelm. in Lemnac. 144. 1868.

Plants solitary or only 2–3 attached; 1.5–3.5 mm. long by 1.0–2.5 mm. wide, usually toward the small range; elliptic-orbicular to obovate, slightly asymmetrical, apex obtuse; dorsal surface medium green, slightly laterally convex, ventral surface strongly red-purple, rounded convex, slightly inflated; nerveless or indistinctly nerved; root sheath short, the young root usually lying in a furrow as described for *L. minor;* rootcap prominent, tip bluntly rounded; margin of frond entire, thin, frequently curling when dried.

Flowers typical of the genus, spathe open only at the top; fruit broadly ovoid with prominent shoulders but not winged, projecting slightly beyond frond margin; a single seed, amphitropous, ribbed; strongly red-purple pigmented in fruit, and in hilum and operculum of seed.

Type locality: New York: New Durham Meadows.

Type collection: Austin 8050 (MO). Type collection examined.

Distribution: Eastern and southern United States, California, and Mexico.

Collections examined: CALIFORNIA: Smith & Nobs 1222 (UC), Nobs & Smith 1496 (FSU), Smith 1495 (FSU); FLORIDA: Godfrey & Redfearn 52845 (FSU), Godfrey 54442, 54666 (FSU), Canby 17 (MO), Troth 23

(FSU), Ramsey 198 (FSU), Hitchcock (F), Standley 73479 (F), Daubs 661, 662, 664, 752, 753, 900, 902 (ILL); IOWA: Graves (MO); LOUISIANA: Reese 1447 (FSU), Egard (MO), Daubs 778, 779, 905, 906, 910, 914, 911 (ILL); ILLINOIS: G. N. Jones 22255 (ILL), Ahles 5244 (ILL), Daubs 863, 869, 872 (ILL); MINNESOTA: Sheldon (MO); NEW JERSEY: Austin 8050 (MO); OHIO: Pieters (US); SOUTH CAROLINA: Godfrey & Tryon 1480 (MO); UTAH: Rydberg & Carlton 6953 (US); BAHAMAS: Britton & Millspaugh 5886 (MICH, F); MEXICO: Dressler 261 (MO), Rose & Hough 4334 (US), Daubs 604, 605 (ILL).

This species partakes of some of the characteristics of both *L. gibba* and *L. minor,* but never attains the size of either of these species. It is more convex beneath and more highly pigmented than *L. minor,* the upper surface frequently showing an abundance of red-purple coloring also, and it does not closely approach the gibbous condition of *L. gibba,* although it has frequently been confused with this species. Flowers and fruits have been observed in the collections of Godfrey (55745, UC) from the St. Marks Wildlife Refuge, Florida. The flowers are typical of the genus, the spathe open only at the top as in *L. minor* and *L. gibba.* The fruit is somewhat intermediate between these two species, being always one-seeded, with broad shoulders but without wings. The seed is ovoid and ribbed, resembling that of *L. gibba.*

L. obscura is certainly closely allied with *L. disperma;* it is indeed doubtful if the two can be consistently distinguished except in the fruiting condition, as the acute-pointed rootcap is the most consistently differing vegetative feature, and even here Hegelmaier describes his variety *fallax* as being obtuse-pointed. Likewise, Giardelli's *L. parodiana,* which I have placed in synonymy with *L. disperma,* is indistinguishable vegetatively. Giardelli reports an occasional one-seeded plant, but since even *L. gibba,* which normally has several seeds, may occasionally appear with only one, these rare occurrences do not justify species recognition. The geographical distribution supports the treatment as given here since *L. obscura* is recognized only from North America and *L. disperma* only from South America and the Australian area.

9. LEMNA MINOR Linnaeus

Plate 7

Lemna minor L. in Sp. Pl. 970. 1753.
Lenticula minor Scop. in Fl. Carn. 2nd ed. 2: 213. 1772.
Lenticula vulgaris Lam. in Fl. Fr. 2: 189. 1778.
Lemna vulgaris Lam. in Encyc. 3: 464. 1791.
Lemna minuta H. B. & K. in Nov. Gen. & Sp. 1: 372. 1815.
Lemna gibba sensu Weber in Mert. and Koch, Roehling's Deutsch. Fl. 3rd ed. 1: 195. 1823.
Lemna palustris Haenke ex Mert. and Koch *loc. cit.* 1823.

Lemna minor var. *minima* Chev. in Fl. Par. 2: 256. 1827.
Lemna obcordata Bojer in Hort. Maurit. 358. 1837.
Lemna ovata A. Br. ex Krauss in Flora 28: 344. 1845.
Lenticula cyclostasa Kurz in Jour. Linn. Soc. London 9: 266. 1867.
Lenticula minima Kurz *loc. cit.*
Lemna monorhiza Montand. in Guide Bot. 308. 1868.
Lemna minor var. *oxymitra* Hegelm. in Lemnac. 143. 1868.

Plants commonly cohering in groups of 2–5; 3.0–6.0 mm. long by 1.5–4.0 mm. wide; very nearly symmetrical, suborbicular to elliptic-obovate in outline; flat to slightly convex on either surface, mostly obscurely three-veined, sometimes with a row of small papules along the median vein; deep green above and tinged with purple or red beneath; the root sheath long, cylindric, and unappendaged; the young root parallel with the lower surface and usually lying in a furrow in the frond tissue; roots long, rootcap bluntly rounded and prominent.

Flowers characteristic of the genus, the saclike spathe open only at the top; ovule solitary, amphitropous; fruit broadly ovoid, wingless, projecting about one-third beyond the frond margin; seed obovate, flattened, smooth, outer coat more or less spongy, hilum pigmented and prominent, operculum lightly pigmented and flattened.

Type locality: Europe.

Type collection: Linnaeus, listed in Savage (1945).

Distribution: Doubtless with the widest distribution of any of the duckweeds; found in almost all temperate and tropical regions of the world, and occurring in Alaska nearly at the Arctic Circle.

Collections examined: UNITED STATES: ALASKA: Calder 5000 (UC), Smith 1893 (UC), Smith 1864 (UC), Smith 2129 (UC); ARIZONA: Gould & Haskell 3264 (UC), Peebles 10635 (MICH), Wiggins 8508 (MICH), Pultz 1786 (F); ARKANSAS: Daubs 829, 830 (ILL); CALIFORNIA: Macbride & Drouet 4546 (F), Bolander 2662 (US), Nobs & Mason 748 (UC), Grant & Schneider 8064 (UC), Mason & Grant 12966 (UC), Pollard (MO, F); COLORADO: Ehlers 687 (MICH), M. E. Jones 603 (MO); CONNECTICUT: Eames (ILL); FLORIDA: Daubs 655, 654, 658, 731 (ILL), Godfrey 56350 (UC), Godfrey 52874, 60607 (FSU), Curtiss 2695 (F), Drouet, Madsen, & Crowson 11502 (F), Godfrey & Lindsey 56834 (FSU, UC); GEORGIA: Duncan 7658 (FSU, UC, MO); HAWAII: Heller 2134 (F, UC, MO), Hitchcock 14120 (US); IDAHO: Ehlers & Erlanson 319 (MICH), Henderson 3965 (US); ILLINOIS: Daubs 523, 528, 545, 807, 860, 867, 873, 875, 876, 878a (ILL), G. N. Jones 16626 (ILL), Ahles 4175 (ILL), G. N. Jones 19773 (ILL), V. H. Chase 10680 (ILL, F); INDIANA: Daubs 501 (ILL), Henderson 61640 (ILL), Lansing 1785, 1625 (F), Standley 92858 (F); IOWA: Hayden 10245 (MO), Fay 658 (UC), Thorne 10660 (FSU), Fink 399 (US); KANSAS: Gates 17583 (MICH),

Bartholomew (MO); LOUISIANA: Daubs 787, 791, (ILL); MAINE: Norton 4 (F, US); MASSACHUSETTS: Bartlett 1181 (ILL), Ogden & Wiggens 1730 (MO, FSU, UC, ILL), Trelease (MO), Torrey, Flint, & Davis (FSU), Fernald 851 (MO); MICHIGAN: Daubs 502, 503 (ILL), Richards 4301 (ILL), Grassl 7638 (MICH), Voss 2921 (MICH), Gillman (MO); MINNESOTA: G. N. Jones 18086 (ILL), Moore & Moore 10404, 11598 (ILL), Moore & Huff 18337, 18653, 18641 (ILL), Moyle 2331 (MO, F); MISSISSIPPI: Daubs 798 (ILL), Steyermark 26563 (UC), Steyermark 20060 (F), Tracy 5013 (F); MISSOURI: Steyermark 71783, 64455, 73596, 28746, 28744, 74103, 72499, 72990 (F), Palmer 56468, 61567 (F), Engelmann (MO), Bush 156/96, 523 (MO), Kellogg 1645 (MO); MONTANA: Umbach 159 (US, F, MICH), Blankenship 488 (US, MO, F); NEBRASKA: Tolstead (MO), Webber (MO); NEVADA: Drouet & Richards 3289 (F); NEW JERSEY: Fogg (ILL, UC), Austin (MO), Adams 2795 (MO); NEW MEXICO: Lindsey 35 (F), Arsene 17629 (US, F); NEW YORK: Daubs 507 (ILL), Leggett (MO, F), Muenscher & Lindsey 3135 (MO, F), Muenscher & Maguire 1039 (MO), Palmer 263 (MO); NORTH DAKOTA: Waldron (MO), Stevens (F); OHIO: Hicks (MO); OKLAHOMA: G. W. Stevens 315 (ILL), OREGON: Abrams 9542, 9743 (MICH), Sheldon 8738 (MO, F, US), Lawrence 1197 (US); PENNSYLVANIA: Wahl 3425 (ILL), Fogg 21123 (UC), Westerfield 5301 (FSU), Drouet 8599, 4871 (F), Small (F), Berkheimer 3422 (F); SOUTH DAKOTA: Over 17187 (US), Williams (US); TENNESSEE: Fisher 2103 (F); TEXAS: Bush 1438 (MO), Palmer 11803 (US), Warnock, Bartley, & Tharp 46433 (F); UTAH: Wooton (US), Maguire 13181 (UC), Drouet, Richards, & Rubenstein 4149 (F), M. E. Jones 5321 (MO), Maguire 2287 (MO); VERMONT: Brandon (MO); VIRGINIA: Fernald & Long 10569 (MO); WASHINGTON: Eyerdam 1725 (ILL), Bardell (MO), Grant (F); WISCONSIN: F. C. Seymore 14732 (ILL), E. J. Hill 188 (ILL), Fassett 4147, 22263, 17427 (MO), Shinners 1121 (UC); WYOMING: Beetle & Snyder 72 (MO), Nelson & Nelson 6424 (MO), Palmer 52661 (F), Porter 5748 (UC).

CANADA: ALBERTA: Breitung 16783 (F), Cody & Loan 3768 (MO); BRITISH COLUMBIA: Macoun 28110, 28103, 88278 (F, US), Murie 1307, 1308 (MO); MANITOBA: Macoun 76886 (MO); NOVA SCOTIA: Steinmetz 1739 (ILL), Fassett 18828 (MO, F), Fowler 8049 (MO); ONTARIO: Shields 433 (MO), Daubs 504, 506 (ILL), Gillman (MO); PRINCE EDWARD ISLE: Fernald & St. John 7125 (US); QUEBEC: Calder 675 (MO), St. John 90284 (UC), Marie-Victorin 8453 (US), Fernald, Bartman, Long, & St. John 7126 (F); SASKATCHEWAN: Macoun 13992b (F), Breitung 4795 (MO).

MEXICO: BAJA CALIFORNIA: Wiggins & Gillespie 3967 (MO); MEXICO: Fassett 2844 (MO); DISTRITO FEDERAL: Daubs 603 (ILL), SAN LUIS POTOSI: Daubs 637 (ILL).

CENTRAL AMERICA: EL SALVADOR: Carlson 1045 (F), Standley 2546 (UC); HONDURAS: Standley & Chacon 5703 (F); NICARAGUA: Standley 2946 (F).

SOUTH AMERICA: BRAZIL: Drouet 2203 (MICH), Sacco 2835 (F); Rose & Russell 19860 (US); URUGUAY: Herter 151a (MO).

BERMUDA: Moore 3021 (F).

EUROPE: AUSTRIA: Keck (MO), Dorfler (MO), Joor (MO); ENGLAND: Newbold (US), Prung (MO); FINLAND: Lindberg 143 (UC); FRANCE: Narjadeae 1015 (MICH), Tidestrom 13285 (F); GERMANY: G. N. Jones 31310 (ILL), Reinsch (US), Gmelin (F), Engelmann, in 1824 (MO); HUNGARY: Steinitz 18437 (ILL); ITALY: Gussome (MO), Ball (F); NETHERLANDS: Florschutz (MO); POLAND: Krawiec (MO); NORWAY: Jordal 686 (F); SWEDEN: Thedinius 93 (MO), Alm 1677 (MO); SPAIN: Normal 39 (F), Trelease 958 (MO); CANARY ISLANDS: Pitard 683 (MO), Gandoger (MO); SWITZERLAND: Castella (US), Bergren 75 (F), Kjallmert (F), Schleicher (UC).

ASIA: CHINA: Beach H–74 (US), Steward 1385 (UC), Metcalf 11027 (UC) same collection as Ling Yu Tai 11027 (MO); INDIA: Rodin 5604 (UC), R. N. Parker 2856 (UC), Koelz 4786 (US, MICH), Koelz 4580 (F, US), Thivy 128 (US); MALAY: Suekele 4428 (UC); PHILIPPINES: Robinson 68473 (US).

AUSTRALIA: Gunn (MO).

NEW ZEALAND: Kirk & Wellington (MO), Setchell (UC), Kirk (F).

AFRICA: CAPE OF GOOD HOPE: Krauss (A. Braun) (MO).

Lemna minor, because of its wide distribution, has been used as a sort of "catch-all" category, and many herbarium specimens which are actually other species have been labeled with this binomial. Infrequently, perhaps inadvertently, it has also been applied to *Spirodela polyrhiza*. It is hoped the treatment of the species as given here may aid in preventing further difficulty in its recognition.

Perhaps the greatest difficulty arises in distinguishing *L. minor* from the flattened forms of *L. gibba*, and indeed positive separation may not always be made. Generally the dark green surface, symmetrical apex, medium size air spaces (in proportion to the size of the frond), and the position of the young root are all definitive for *L. minor*. These contrast with the mottled lighter green surface, asymmetrical apex, and large air spaces of *L. gibba*. In addition the reproductive pouches of *L. gibba* usually extend farther up the frond margin, and the margins of the pouches are thin and curl on drying.

Landolt (1957) identified a *L. minor* I and a *L. minor* II on the basis of certain morphological and physiological characteristics. I have examined a number of each of these and almost without exception would consider

his *L. minor* II as being typical of the species as described here. His *L. minor* I is more nearly typical of the flat form of *L. gibba* as described herein. Also, both the pigmentation and blooming habits as described by Landolt would support this treatment. I have not seen this form in flower or fruit.

10. LEMNA PERPUSILLA Torrey

Plate 9

Lemna perpusilla Torr. in Fl. N.Y. 2: 245. 1843.
Lemna minor Griff. (non L.) in Notul. 3: 216. 1851.
Lemna paucicostata Hegelm. in Lemnac. 139. 1868.
Lemna angolensis Welw. ex Hegelm. in Lemnac. 141. 1868.
Lemna aequinoctialis Welw. ex Hegelm. *loc. cit.* 142. 1868.
Hydrophace perpusilla Lunell in Amer. Mid. Nat. 4: 237. 1915.
Lemna minima Blatt. & Hallb. in Jour. Ind. Bot. 2: 50. 1921.
Lemna blatteri McCann in Jour. Bombay Nat. Hist. Soc. 93: 154. 1942.
Lemna eleanorae McCann *loc. cit.*

Plants solitary or 3–5 connected; 1.0–2.5 mm. long, 0.7–2.0 mm. wide; obovate to orbicular obovate, strongly asymmetrical; upper surface convex with a prominent papilla at node and apex, usually with smaller papillae along the center nerve; nerves 1–3, indistinct, or nerveless; lower surface more or less convex; light to medium green in color, not pigmented; root sheath winged, often prominently; root tip usually slightly curved, rootcap acute.

Flowers characteristic of the genus; spathe open, style long, lateral or oblique; one ovule, obliquely orthotropous; fruit asymmetrical, lying obliquely in the pouch, lateral style persistent; seed ovoid, prominently ribbed, pigmented in hilum and operculum.

Type locality: New York: Staten Island.

Type collection: John Torrey, in 1829 (MO). Collection examined.

Distribution: To some extent in all temperate or tropical regions of the world, but more abundantly in the Western Hemisphere.

Collections examined: ARIZONA: Gould & Robbins 3607 (UC, US), Drouet, Richards, Darrow & Darrow 3374 (F, MICH), Gooding 412–45 (MICH); ARKANSAS: Daubs 829, 832, 851, 852 (ILL), Eggert (MO); CALIFORNIA: Clokey & Thompson 4630 (UC), Mason 13009 (UC), S. G. Smith 725 (FSU); DELAWARE: Commons 2 (MO); FLORIDA: Curtiss 4543 (US, MO, F), Muenscher 14254 (UC), Godfrey 54518, 60648, 60647 (FSU), Godfrey 56350 (US, MO), Daubs 653, 904, 900 (ILL); GEORGIA: Ravenel (US), Harper 433 (MICH); ILLINOIS: Daubs 862 (ILL), Ahles 2566 (ILL), Patterson (US), Eggert (US, MO), Schneck (ILL, MO), Hall (MO), Engelmann (MO); IOWA: Anderson (MO); LOUISIANA: Kral 8203c (FSU), Reese 1447 (FSU); MICHIGAN: Rapp

3268 (MICH); MISSISSIPPI: Tracy 5013 (F, US); MISSOURI: Tracy (US), Bush 584 (US), Steyermark 27930 (F), Henney & Thompson (MO), Eggert (MO), Thompson (MO), Mackenzie (MICH); NEW YORK: Allen (F), Miller (F), Torrey (MO); OKLAHOMA: Harding 419 (MICH, UC); PENNSYLVANIA: Small (F), Austin (F), Commons 1 (MO); TENNESSEE: Curtiss 2693 (F), Austin (US), Gattinger 2693 (US); TEXAS: Runyon 4158, 4201, 3937 (MICH), Fisher 41272 (US); VIRGINIA: Coville 35 (US); MEXICO: Palmer 177 (MICH), Bailey 237 (F), Fassett 28457, 28444 (F), Rose & Hough 4440 (US), M. E. Jones 23465 (UC), Wright 1248 (F, UC), Drouet 3721 (MICH, US, MO, F), Steere 1567 (MICH).

CENTRAL AMERICA: EL SALVADOR: Fassett 28543, 28541, 28816, 28347 (F), Standley & Padillo 2528 (F); GUATEMALA: Sharp 4535 (F), Kellerman 6651 (F), Standley 89331, 62656, 64059, 64060, 64658 (F); HONDURAS: J. D. Smith 2201 (US), Standley 53790 (F).

SOUTH AMERICA: ARGENTINA: Pedersen 3989 (MO); BOLIVIA: Cardenas 2612 (F); BRAZIL: Drouet 2203 (F), Rose & Russell 19858 (US); COLOMBIA: Hermann 11312 (MICH); ECUADOR: Svenson 11024 (UC, US), Hitchcock 20076, 21258 (US); GALAPAGOS: Svenson 87 (MO, UC); PERU: Hermann 11313 (MICH), Ferrera 10608 (US).

WEST INDIES: CUBA: Wright 71, 3215 (MO), Wright 3722 (US), Ekman-Urban 3003 (F), Shafer 10596 (F); CURACAO: Britton & Shafer 2293, 2294 (F); GRENADA: Broadway 1731 (F); HAITI: Eyerdam 344 (F), Bartlett 17293 (US, MICH); JAMAICA: Britton 2835, 1696 (MO); PUERTO RICO: Daubs 883 (ILL), Britton & Shafer 1886 (F, MO), Britton, Britton & Brown 6765 (F); TRINIDAD: Broadway 2354 (F, MO).

ASIA AND PACIFIC: FIJI ISLANDS: Wilkes Exp. (US); FORMOSA: Koto-Syo (UC); INDIA: Thivy 124, 127 (MICH); MADAGASCAR: Rensch 3520 (US); NEW CALEDONIA: Balaura 3112 (UC); PHILIPPINES: Robinson 58431–2, 17297 (US), Merrill 4437 (US), Merrill 131 (MO, US, F), Mcgregor 2–326 (US); TONGA: Setchell 647 (MO), Setchell & Parks 15647, 15540 (UC).

EUROPE: FRANCE: Questel 345 (US).

AFRICA: RHODESIA: Wildenow (?) 4264 (MO); GOLD COAST: Baldwin 13466 (MO).

Lemna perpusilla has perhaps the smallest plants of any species of the genus, and has often been mistaken for *L. minima*, from which it may be readily distinguished by the winged root sheath, prominent papillae, and asymmetrical outline. It is also the most frequently flowering and fruiting species of the family and is often collected in one or both of these conditions.

Thompson (1898) has previously placed *L. paucicostata* in synonymy with *L. perpusilla*, and this treatment has been generally accepted by

Western authors. An exception to this has been Giardelli, who has annotated many herbarium specimens with the former binomial, and also used it in her treatment of the Lemnaceae in *Flora of Guatemala* (Standley and Steyermark, 1958). I have identified many of her specimens as being *L. trinervis* as treated here. Only occasionally are the plants not distinctly three-nerved but otherwise they partake definitely of the species characteristics. Thompson (*loc. cit.*) recognized Austin's original designation of *L. perpusilla* var. *trinervis* but did not further discuss the synonymy. From Hegelmaier's descriptions and drawings, and more particularly from a study of specimens cited by him, I have also come to the conclusion that *L. paucicostata* should be placed in synonymy with *L. perpusilla.*

Hegelmaier (1868) has also placed *L. aequinoctialis* in synonymy with *L. angolensis*, this latter binomial applied by Welwitsch to a collection made in Angola, Africa. While these plants have prominent papillae at both the node and apex, these are no more prominent than many typical plants of *L. perpusilla.* Since they do not differ noticeably or consistently in any other characteristics I have placed these two binomials in synonymy with *L. perpusilla.*

11. LEMNA TRINERVIS (Austin) Small

Plate 13

Lemna perpusilla var. *trinervis* Austin in A. Gray Man. Bot. 5th ed. 479. 1867.
Lemna paucicostata var. *membranacea* Hegelm. in Lemnac. 141. 1868.
Lemna trinervis (Austin) Small in Fl. S.E. U.S. 230. 1903.

Plants solitary or 2–4 attached; 2.5–5.0 mm. long, 1.5–3.0 mm. wide; obovate, apex obtuse, base subacute, very nearly symmetrical; thin and membranous, flat on both surfaces, papillae lacking or at least not prominent; three distinct and prominent nerves; root sheath winged, rootcap acute; light to medium green, not pigmented.

Flowers characteristic of the genus, spathe open; fruit ovoid-oblong, slightly oblique to straight in the pouch; ovule orthotropous, slightly oblique; seed elongate-ovoid, ribbed and transversely striate.

Type locality: Pennsylvania, Wayne County.

Type collection: Austin, Oct. 1860, in flower and fruit (MO). Type examined.

Distribution: Chiefly in eastern and southern United States, Mexico, and Central America. Also from northern South America, Hawaii, and India.

Collections examined: UNITED STATES: ARIZONA: Gould & Haskell 3264 (US); ARKANSAS: Daubs 825, 836, 838, 826, 831 (ILL); FLORIDA: Daubs 760, 903 (ILL), Hitchcock 373 (F, US), Godfrey 56251, 60602

(FSU), Godfrey 56331a (MO, FSU), Godfrey & Reinert 61140 (FSU); GEORGIA: Austin (US), Harper 433 (F); HAWAII: Heller 2134 (MICH, F); ILLINOIS: Schneck (ILL), Ahles 2980 (ILL); KANSAS: Hitchcock 848 (MO); MASSACHUSETTS: Ogden & Wiggins 1730 (MICH); MISSISSIPPI: Ray 8163 (FSU), Daubs 797 (ILL); MISSOURI: Bush (US), Palmer & Steyermark 41418 (MO), Trelease (MO); NEW YORK: Miller (US); OKLAHOMA: Daubs 859 (ILL), Stevens 1883 (ILL); PENNSYLVANIA: Austin (MO); TENNESSEE: Gattinger (MO), Gattinger 28 (US); TEXAS: Palmer 14254 (MO).

MEXICO: Rose & Painter 6877 (US), Daubs 635 (ILL), Rose, Standley & Russell 13990, 14385 (US), Wiggins & Rollins 366 (MO), Daubs 609 (ILL), Gaumer 1437, 2393 (F, MICH, US, MO), Steere 1236 (MICH).

CENTRAL AMERICA: EL SALVADOR: Fassett 23834, 28575 (F), Fassett 28266 (MO, MICH, F), Standley 23157, 22445, 20334, 20564, 21143, 22015, 24012, 24541 (US), Calderon 1483 (US); GUATEMALA: Bartlett 12781 (MICH, US), Steyermark 47697 (F), Standley 89409, 59851 (F); NICARAGUA: Standley 9239 (F), Baker 2390 (MO).

WEST INDIES: CUBA: Shafer 10596 (MO), Acuna (MICH), Walker (MICH); JAMAICA: Fassett (F), Harris & Fassett (MO); HAITI: Eyerdam 344 (US, MICH); TOBAGO: Broadway 3103 (F, MO).

SOUTH AMERICA: COLOMBIA: Fassett 25362, 25379 (US); VENEZUELA: Gines 3893 (US); BRITISH GUIANA: Hitchcock 16622 (US).

INDIA: Koelz 4580 (MICH), Thivy 100, 101, 126 (MICH).

Some discussion of this species has been made under the treatment of *Lemna perpusilla*, from which species Austin first separated it as a variety. Only in the narrowly winged root sheath and acute rootcap does it resemble this species. Its other morphological characters, both vegetative and fruiting, seem to justify Small's elevation to species rank. It is usually readily recognizable on sight by the three prominent nerves although some of the tropical specimens are less distinctly nerved. These latter are frequently very thin and perhaps are Hegelmaier's variety *membranacea*. Many of them have been labeled on herbarium sheets as *L. paucicostata*.

Lemna trinervis may occasionally be confused in the fruiting form with *L. valdiviana* but is distinguishable from this species by its winged root sheath. Of apparent tropical affinity, it is abundant in Central America, and occurs frequently throughout the remainder of its range.

12. LEMNA VALDIVIANA Philippi

Plate 10

Lemna valdiviana Phil. in Linnaea 33: 239. 1864.

Lemna torreyi Austin in A. Gray Man. Bot. 5th ed. 479. 1867.

Lemna valdiviana var. *pellucida* Hegelm. in Lemnac. 138. 1868.

Lemna valdiviana var. *platyclados* Hegelm. in Bot. Jb. (Engler) 21: 298. 1896.

Lemna valdiviana var. *abbreviata* Hegelm. *loc. cit.*
Lemna cherokensis Schweinitz ex Hegelm. *loc. cit.*
Lemna cyclostasa Ell. ex Thomp. in Rep. Mo. Bot. Gard. 9: 35. 1898.

Plants floating on surface or submersed; 2–10 remaining attached; 2.5–5.0 mm. long, 0.5–1.5 mm. wide; oblong, in fruit elliptical to obovate in outline; symmetrical except at base which may be strongly asymmetrical; both surfaces flat or nearly so, upper rarely with minute papillae; nerveless or indistinctly one-nerved; root tip and rootcap round pointed, frequently strongly curved; frond uniformly light green, not pigmented.

Flowers typical of the genus, spathe open; fruit elongate-ovate, long exserted, style obliquely terminal and persistent; fruit straight in the pouch; ovule orthotropous; seed oblong-ovoid, ribbed and transversely striate, operculum pointed and prominent.

Type locality: Chile: province of Valdivia.

Type collection: Philippi, in 1864, duplicate in Mo. Bot. Gard. Herbarium. Collection examined. Other collections cited by Hegelmaier and examined include: Austin, New Jersey (MO), Coues, Arizona (MO), Lindheimer, Texas (MO), Hahn, Mexico (MO, US).

Distribution: Western Hemisphere, chiefly eastern and southern United States; Mexico and Central America; South America.

Collections examined: UNITED STATES: ARIZONA: Phillips 2587 (UC, MO, MICH), Gould 5230 (UC), Coues & Palmer 451 (MO); ARKANSAS: Eggert (MO), Daubs 827, 828, 830, 839, 844, 848 (ILL); CALIFORNIA: Congdon (US), Nobs & Smith 1579, 1889, 1861, 1630, 1420 (UC), Nobs & Smith 1496 (FSU); CONNECTICUT: Eames (US); FLORIDA: Daubs 753, 754 (ILL), Hitchcock 373 (F, MO), Hitchcock 2025 (F), Godfrey 56257 (UC, FSU), Godfrey & Redfearn 52845 (FSU), Godfrey 57712, 58201, 52863a (FSU), Drouet, Madson & Crowson 11508 (F); GEORGIA: Ravenel (MO), Harper 424 (MO), Harper 120 (MO, F, MICH), Trelease (MO); INDIANA: Clark 19 (US); ILLINOIS: Daubs 865 (ILL), Swayne (ILL), Moffatt 286 (ILL); LOUISIANA: Daubs 781, 910 (ILL), Langlois (ILL), Reese 1626 (FSU), Austin (MO), Trelease (MO), Palmer 8923 (MO); MASSACHUSETTS: Kennedy (MO, US), Fernald 851 (MO), Churchill 259 (MO), Blake 1578 (US); MISSISSIPPI: Tracy 5013 (MO), Fassett 19912 (MO); MISSOURI: Steyermark 20902, 11943, 12793 (MO), Trelease 202/09 (MO), Palmer & Steyermark 41699 (MO), Redfearn 5743 (FSU); NEVADA: King & Bateson (MO); NEW JERSEY: Austin, in 1862 (MO), Austin, in 1867 (US, MO); NEW MEXICO: Metcafe 407 (MO); NEW YORK: Young (MO, US), Muenscher & Curtis 6785 (UC); OHIO: Hicks (MO), Haecker (MO); OKLAHOMA: Waterfall 10438 (UC); RHODE ISLAND: Collins (MO); SOUTH CAROLINA: Ravenel 191, 1992 (MO), Tarbox 992 (US), Godfrey & Tryon 721 (US, MO); TENNESSEE: Everman, in 1893 (F); TEXAS: Daubs 855 (ILL),

Sperry T1395 (MICH), Palmer 34477 (US, F), Tweedy 3 (US), Palmer 34478 (MO), Reverchon, in 1900 (MO), Trelease (MO); UTAH: Garrett 6683 (F); VIRGINIA: Fernald & Long 10175 (US, F, MO); WYOMING: Rose 401 (US).

MEXICO: Hahn, several collections (MO, US), Fassett 28399 (MICH), Pringle 7301 (F, MICH), Fassett 28457 (MO).

CENTRAL AMERICA: EL SALVADOR: Fassett 28166 (MICH); PANAMA: Bartlett & Lasser 16825, 16979 (MICH).

SOUTH AMERICA: ARGENTINA: Kurtz 6991a (MO); CHILE: Philippi, in 1864 (MO); BRAZIL: Reitz & Klein 1678 (US), Smith & Reitz 9887 (US).

WEST INDIES: BERMUDA: Britton & Brown 1175 (F, US); JAMAICA: Harris 10837 (US).

Lemna valdiviana is usually easily recognized by its elongate form, light green appearance, and tendency to form colonies through the coherence of several successive generations. This latter characteristic is particularly helpful in distinguishing it from *L. minima,* which seldom has more than two fronds attached, the younger frond appearing more nearly basal than lateral.

The binomial *Lemna cyclostasa* Ell. ex Thompson is included here as a synonym *sensu* Thompson. The epithet *cyclostasa* was first applied by Elliott (1824) as a variety of *L. minor.* In his description, however, he used it only as a term to describe a plant he remembered from boyhood and was not applying it to a specific taxon. Thompson accepted the combination of *L. cyclostasa* as valid, ascribing it to Chevalier (1827) who had no such species. The error has generally been perpetuated since 1898.

The varietal names of Hegelmaier have also been reduced to synonymy, not that the variation is not recognizable but rather that it does not seem consistently classifiable. (See Plate 11 and discussion under *L. minima.*) That the fruiting plants are more uniform in their vegetative morphology is further reason for adoption of this point of view.

The binomial *Lemna cherokensis* Schweinitz ex Hegelmaier is included in the synonymy, being also so placed by Hegelmaier. Neither the binomial nor any description appears to have been published by Schweinitz, nor is any specimen cited by Hegelmaier, so the exact nature of the taxon is in doubt.

13. LEMNA MINIMA Philippi

Plate 11

Lemna minima Phil. in Linnaea 33: 239. 1864.
Lemna valdiviana var. *minima* Hegelm. in Lemnac. 138. 1868.
Lemna miniscula Herter in Rev. Sudam. Bot. 9: 185. 1954.

Plants frequently solitary, seldom more than 2 remaining connected; 1.0–2.5 mm. long, 0.7–1.5 mm. wide; ovoid to elliptical in outline, asymmetrical, both base and apex obtusely rounded; flat to very slightly convex on both surfaces, occasionally a few low papules on median line of upper surface; nerveless or indistinctly one-nerved; air spaces small, uniform, in central area only; margin thin, entire; light to medium green in color, not pigmented; reproductive pouches small, young plants appearing more basally than laterally attached.

Flowers typical of the genus, spathe open; fruit long-exserted, elongate, tapering to the terminal and persistent style, ovule orthotropous; seed elongate, ribbed, transversely striate, operculum pointed, prominent.

Type locality: Chile: Santiago.

Type collection: Philippi, cited by Hegelmaier (1868), in Berlin Herbarium, probably lost. A collection from California (Bolander, MO) also cited by Hegelmaier has been examined.

Collections examined: ARGENTINA: Krapovickas (F), Eyerdam & Beetle 22416 (F, MICH, UC); CHILE: Johnston 6912 (US, F), Skottsberg 871 (F), Belem (UC); URUGUAY: Rosengurtt B1682 (US), Herter 1512 (UC), Herter 151 (MO).

UNITED STATES: CALIFORNIA: W. Thompson 208 (US, MO), McMurphy 129 (US), Mason 11545, 12926 (UC, MICH), Mason & Smith 8326 (UC), L. Koch 1011 (ILL), Wiggins 3053a (UC), Abrams 3758 (MO), Henney 107, 113, 946 (MO), Congdon (MO), W. Thompson 67, 96 (MO), Hansen 482 (US), Bolander (MO), Blankenship (MO), C. H. Thompson, several (MO), Pollard (MO), Tharp (MO), Nobs & Smith 993, 1496 (FSU); NEW MEXICO: Metcafe 407 (MICH, ILL); NEVADA: Gooding 935 (MO); TEXAS: Tharp (MO), Palmer 11803 (MO); UTAH: M. E. Jones 5983g (MO, MICH), Muenscher 2285 (MO).

Many herbarium specimens of *Lemna perpusilla* are mislabeled *L. minima*, the error doubtless arising from the small size of the plants of these two species. The typical *L. minima*, easily recognized by its symmetry, thin margin, and small basal reproductive pouches, may be specifically separated from *L. perpusilla* through the lack of wings on the root sheath. Similarly *L. minima* is usually easily distinguished from *L. valdiviana*, which is elongated in form, asymmetrical at the base, and generally has large numbers of plants cohering. These two species do, however, intergrade in form and in flowering and fruiting characteristics, which makes them occasionally difficult to separate. The fruit and seed of *L. minima* are slightly smaller in circumference and thus appear more elongate than those of *L. valdiviana*, and also the style is usually more nearly terminal, this frequently being laterally directed in *L. valdiviana*. In *L. minima* also, the fruit may be directed outward from the base of

the plant nearly in line with the plant axis, similar to the manner of attachment of the young frond.

The geographical distribution of *L. minima* is more restricted. I have recognized it only from the western part of the United States, chiefly California, and in South America only from Chile, Argentina, and Uruguay. *L. valdiviana* has a greater area of distribution in eastern and southern United States and Mexico, and is also more frequently encountered within its range.

Hegelmaier, in his monograph (1868), recognized *L. minima* only as a variety of *L. valdiviana*, although later (1896) he accepted its species designation with some misgivings. The evidence as presented here is that both species are valid and both are thus recognized.

14. LEMNA TRISULCA Linnaeus

Plate 6

Lemna trisulca L. in Sp. Pl. 970. 1753.
Lenticula trisulca Scop. in Fl. Carn. 2nd ed. 2: 213. 1772.
Lemna cruciata Roxb. in Hort. Beng. 66. 1814; Fl. Ind. 3: 566. 1832.
Lemna intermedia Ruthe ex Schleid. in Linnaea 13: 392. 1839.
Staurogenton trisulcus Schur in Verh. siebenb. Ver. Naturw. 4: 70. 1853.
Lemna bisulca Veesenm. in Beiträge Pfl. Russ. Reich. 9: 104. 1854.
Lemna trisulca var. *linearis* Asch. & Graebn. in Syn. Mitt. Eur. Fl. 2: 392. 1904.

Plants remaining attached in large numbers, forming extensive tangled masses, submersed except when flowering; 5.0–20.0 mm. long including the elongate stipe, 2.5–5.0 mm. wide; symmetrical, elongate-lanceolate, base tapered acute with long attenuate stipe; flat on both surfaces; air spaces in central area only; one nerve prominent, two lateral nerves indistinct; roots often lacking, but when present long with acute pointed rootcap; margin of apex serrate.

Flowers typical of the genus and the flowering plants also more nearly typical, being short stipitate and usually 2–3 cohering, floating on the surface; flower spathe open; fruit one-seeded, amphitropous; seed ribbed.

Type locality: Europe.

Type collection: None listed in Savage (1945).

Distribution: Common in the temperate zone of the Northern Hemisphere; rare in the tropics; apparently lacking in South America.

Collections examined: UNITED STATES: ALASKA: Smith 1863, 2080, 1994, 2239, 2301 (UC); ARKANSAS: Blankenship, in 1888 (MO); CALIFORNIA: Nobs & Smith 1076 (ILL), Mason 14638, 14320 (UC), Austin 238 (MO), Wheeler 4015 (MO); COLORADO: Baker 389 (US), Hermann 5473 (F), Gooding 1788 (MO), Baker 386 (MO); CONNECTICUT: Wright (MO); DELAWARE: Canby (F); FLORIDA: Daubs 658 (ILL); ILLINOIS: V. H. Chase 10684 (ILL), Hill (ILL), Daubs 807, 872 (ILL),

Hall (F, MO); INDIANA: Umbach (F), Clark 1590 (US), Henderson 61–641 (ILL), Buser 1596 (ILL), Harper (F); IOWA: Burk 616 (ILL), Hayden 754 (MO), Shimek (MO), Fitzpatrick (F); MASSACHUSETTS: Seymour 260 (MO), Churchill (MO), Hoffman (MO); MICHIGAN: Gillman (MO), Wight 14, 104, 1397 (US), Anderson (F), Grassl & Tarzwell 7639 (MICH), Eschmeyer 594, 590 (MICH), Farwell 8298 (MICH), Voss 6643 (MICH); MINNESOTA: J. W. & M. F. Moore 10449 (ILL), Moore & Huff 18469 (ILL), Kibichek 119 (US), Cohen, Cohen & Drouet 5289 (F), Richards 1420 (F); MISSOURI: Steyermark 11926, 12419, 14344 (MO), Bush 1495 (MO), Thompson (MO), Williams 1751 (MO), Bush 536 (UC); MONTANA: Whitford 316 (F), Blankenship 489 (F), Umbach 216 (MICH, US), Maguire 627 (UC); NEBRASKA: Webber (MO), Hayden (MO), Williams (MO); NEVADA: Mason 12105 (MO, MICH); NEW JERSEY: Martindale (MO); NEW MEXICO: Fendler 1007 (MO); NEW YORK: Britton (F), Elwert & Svenson 6115 (MO), Muenscher & Lindsey 3136 (MO), Eames 7817 (MO), Haberer 977 (US); NORTH DAKOTA: Lunell (ILL), Bergman 2159 (MO), Mabbot 502 (US); OHIO: Hicks (MO), Thompson (MO); OREGON: Sperry & Martin 770 (US); PENNSYLVANIA: Berkheimer 2943 (UC), Wahl 4400 (ILL); SOUTH DAKOTA: Over 17188, 17189 (US); UTAH: Maguire 3272 (MO), M. E. Jones 6019 (MO), Ward (F, ILL); VERMONT: Dutton (MO), Ahles 6467 (ILL); WASHINGTON: Bardwell (MO), Zeller (MO); WISCONSIN: Fassett 4136 (MO), Bebb 1520 (F), Heddle 1T145 (F), Benke 6268 (F), Hollister 56 (US); WYOMING: Williams 2500 (UC), A. Nelson 2284 (F, MO), A. Nelson 9660 (US, MO), Gooding 1516 (MO).

CANADA: ALBERTA: Brinkman 442, 2192 (US); BRITISH COLUMBIA: Calder, Parmelee, & Taylor 18346 (UC), Hitchcock & Martin 7495 (MO); MANITOBA: Rossback 76 (UC); ONTARIO: Gillett 2139 (MO), Calder 632 (MO), Umbach (F), Marie-Victorin 15723 (F), Daubs 505 (ILL); QUEBEC: Churchill 11259 (MO), Marie-Victorin 25592 (MO), Fernald 7122 (US); SASKATCHEWAN: Clokey 1651 (UC), Macoun 13993 (MO); YUKON: Porsild & Breitung 11527 (UC).

MEXICO: DISTRITO FEDERAL: Hahn (MO), Vigener (MICH); BAJA CALIFORNIA: Wiggins & Demaree 4874 (F, UC), Bell & Newcomb 1373 (F, UC, MO); COAHUILA: Rose & Russell 24226 (US), Fassett 28399 (MICH).

EUROPE: AUSTRIA: Keck (MO), Joor (MO); BELGIUM: Pease 8399 (F); DENMARK: Mortenson (MO); ENGLAND: Burton 430 (F), Bennett 813 (US); FINLAND: Boldt (MO), Florschutz & Kramer (MO); FRANCE: Gandoger (MO), Chassagne 1376 (MO), Copineau (US), Shimper (F), Jeanpert (F), Gandoger 1098 (MO); GERMANY: Engelmann, in 1825 (MO), Reinsch (US), Hegelmaier (?), in 1863 (MO); HUNGARY: Goehring 715 (MO), Dorfler (MO), Steinitz (US), Filarsky &

Kummerle (MO, ILL, F); ITALY: Savi 2003 (F), Mall (MO), Martelli (MO); NETHERLANDS: Boetje & Van Ruyven (F); POLAND: Krawiec (MO); WESTERN SIBERIA: Mameev 699, in 1949 (US); SWEDEN: Fahlander (ILL, F), Ahlberg (MO); SWITZERLAND: Boissiet (MO).

AFRICA: BRITISH EAST AFRICA: Dummer 4578 (US); UGANDA: Loveridge 488 (MO).

ASIA: CHINA: Tsu 125 (UC); JAPAN: Togasi 389 (UC, MICH, F, MO); PERSIA: Hohenacker (MO), Kotschy (MO); PHILIPPINES: McGregor 86219 (US).

Lemna trisulca is easily recognized by its long, attenuate stipe, submersed position, and tendency for many generations to remain connected. The flowering fronds are readily separable from other species of the genus by the serrate margin.

Hegelmaier (1896) recognized a *Lemna tenera* as described by Kurz from a single collection in India, although Kurz appears never to have published the binomial. From his description as quoted by Hegelmaier it appears to closely resemble *L. trisulca*. Inasmuch as no voucher specimens are known nor are any further collections resembling the description in detail (i.e., with entire margins) reported, the validity of the species must remain in doubt.

Description of Genus *Wolffiella*

Wolffiella Hegelm. in Lemnac. 131. 1868.

Plants flat, thin, membranous; elongate or straplike, frequently falcate; solitary or commonly 2 remaining attached, sometimes many remaining connected and forming extensive colonies; without roots; usually submersed except for a small area at the base, the emersed area with a variable number of stomata; more or less punctate with brown pigment cells in epidermis of both surfaces; aerenchymatous tissue present in all species; plants commonly reproducing by budding from a single triangular (in outline) basal pouch.

Flowering rarely, apparently unknown in two species (*W. gladiata, W. denticulata*); flowering cavities on upper surface at one side of median line, or in one species (*W. welwitschii*), on each side; flowers not enclosed in a spathe, unisexual, consisting of a single stamen or a single pistil; anther about ⅓ mm. in diameter, opening along a pigmented line of dehiscence across the top; pistillate flower with a single orthotropous ovule, short style, circular concave stigma; stigma prominently pigmented; pollen scanty (ca. 150 grains per anther), spinulose, 16–22 microns in diameter.

Fruit a slightly laterally compressed utricle with the style persistent; seed smooth, with spongy outer coat; operculum flattened, prominent.

Hegelmaier (1868) originally proposed *Wolffiella* as a subgenus of

Wolffia but later (1896) elevated it to generic rank, although continuing to refer to it as the "zweifelhafte Gattung." In it he included only those forms not known to flower, retaining in the genus *Wolffia* the species *W. welwitschii* even though its affinity seems clearly with other members of *Wolffiella*. Separation into two genera seems completely justified on vegetative morphology alone; the genus *Wolffia* consists of small spheroid plants usually less than 1 mm. in diameter; and the two separate genera are here so recognized.

With the exception of *W. denticulata*, known only from a single collection in South Africa, and a single report of *W. welwitschii* from Angola, Africa, the genus *Wolffiella* is exclusive to the Western Hemisphere, having the most restricted distribution of any genus of the family. It is most abundant in the tropical and temperate areas of Central America, Mexico, and the southern United States. The infrequency of flowering with the resultant seed, and the absence of any specialized overwintering form, perhaps account for its limited distribution.

KEY TO SPECIES OF *Wolffiella*

1. Plant slender, elongate, falcate or doubly so, several times (ten or more) as long as broad.
   2. Margin entire, many plants cohering in colonies.
      3. Base broad, tapering quickly to the rounded apex, plants slightly falcate. . . . . *W. gladiata*
      3′. Base narrow, gradually tapering to a slender sharp point at the apex, plants usually doubly falcate. . . *W. floridana*
   2′. Margin denticulate at tip, plants not cohering in colonies. . . . . *W. denticulata*

1′. Plants broader, shorter, up to seven times (usually less) as long as broad.
   4. Fronds strongly curved, 2 attached forming a segment of a circle, lingulate. . . . . *W. lingulata*
   4′. Fronds flat or only slightly curved.
      5. Stipe nearly median, plant membranous, reproductive pouch shallow. . . . . *W. welwitschii*
      5′. Stipe lateral, frond thicker, reproductive pouch as deep as wide. . . . . *W. oblonga*

15. WOLFFIELLA WELWITSCHII (Hegelm.) comb. nov.

Plate 16

Wolffia welwitschii Hegelm. in Jour. Bot. 3: 114. 1865; Lemnac. 130. 1868.
Wolffia conguensis Welw. ex Trimen in Jour. Bot. 4: 223. 1866.
Wolffiella welwitschii (Hegelm.) comb. nov.

Fronds symmetrical, flat, thin, rectangular to almost square; solitary or

2–3 cohering; individuals 5–6 mm. long by 3–4 mm. wide; margins entire but slightly curled; air spaces only in basal one-third of frond; reproductive pouch shallow, base much wider than the sides; abundantly punctate at margins and base; stipe median or nearly so.

Two flowering cavities, one each to the right and left of the median line, flowers penetrating the upper surface, each pouch with one pistillate and one staminate flower not enclosed in a spathe; flowers and fruit characteristic of the genus.

Type locality: Africa: Angola.

Type collection: Welwitsch 209. This collection from Angola identified by Hegelmaier is in the Missouri Botanical Garden Herbarium and has been examined. It may be a part of the original collection. Also cited by Hegelmaier (1868) is a collection from Cuba, Wright 70, in the above herbarium, which has been examined.

Distribution: Angola; Dominican Republic, Cuba, Ecuador, Guatemala.

Collections examined: AFRICA: ANGOLA: Hegelmaier (?) (MO). CUBA: Austin 3215 (MO), Wright 70 (MO); DOMINICAN REPUBLIC: Fuertes (MO); ECUADOR: Hitchcock 20096 (US); GUATEMALA: Steyermark 31812 (F).

Hegelmaier (1865) placed this species in the genus *Wolffia* on the basis of its bilateral symmetry, characteristic of only some members of this genus, and on its known flowering condition as opposed to the belief at that time that no species of *Wolffiella* produced flowers. The discovery of flowering in three species of this latter genus (reported elsewhere in this treatise) nullifies this latter argument. The number of flowering cavities (two) differs from the characteristic number (one) of the genus *Wolffiella* but does not serve to identify this species with *Wolffia*, no species of which has more than one. The lateral position of the flowering cavities is more nearly characteristic of the genus *Wolffiella*, all of which have this feature, whereas only two species of the genus *Wolffia* exhibit it. The floral and fruiting structures of *W. welwitschii* are quite characteristic of the genus *Wolffiella* but these are rather uniform throughout both genera and have little or no taxonomic value. It is essentially the vegetative characters, the thin, flat membranous frond so characteristic of the genus, which place this species in the genus *Wolffiella*. The species is readily recognized and presents no difficulties except as discussed under *W. lingulata*.

16. WOLFFIELLA LINGULATA (Hegelm.) Hegelmaier

Plate 15

Wolffia lingulata Hegelm. in Lemnac. 132. 1868.
Wolffiella lingulata (Hegelm.) Hegelm. in Bot. Jb. (Engler) 21: 303. 1896.

Plants solitary or usually only 2 remaining connected, infrequently

forming colonies; the 2 connected fronds strongly curved, forming a band with only the base of the parent plant emersed; lateral margins of the plants upturned, tongue-shaped; single plants 3.5–7.5 mm. long, 1.5–4.0 mm. wide, very thin in appearance, base oblique, apex rounded or sometimes dying and dropping off, giving a truncated appearance; air spaces only in the basal one-third of the plant; reproductive pouch nearly equilaterally triangular in outline, stipe at one side or near the corner of the pouch; plants moderately punctate on both surfaces with brown pigment cells.

Flowering cavity to one side of the reproductive pouch, opening on the surface; flowers and fruit typical of the genus; stomata more numerous on emersed surface of flowering plants.

Type locality: Mexico, "near the capital." (See discussion under *W. gladiata*.)

Type collection: Hahn (MO, F). Collection examined.

Distribution: California, Louisiana; Mexico, Panama; Argentina, Uruguay.

Collections examined: CALIFORNIA: C. H. Thompson (MO), Carter 3453 (US, MICH, MO, ILL), Nobs & Smith 675 (UC), Mason 11850, 11548 (UC), Mason 12072 (UC, MICH), Mason & Smith 8227 (FSU), Howell 10790 (UC, F), Parish 4586 (UC), Condit (UC); MEXICO: Hahn (US, MO), Rose & Hough 4547 (US), Pringle 7301 (MICH), Daubs 603, 604, 605, 616, 618 (ILL); PANAMA: Bartlett & Lasser 16506 (MICH); LOUISIANA: Oberholser (UC, US), Daubs 909 (ILL); URUGUAY: Herter 151 (MO).

Distinguishing characteristics of this species are the concave surface and the almost complete circle formed by the attached parent and offspring fronds. In all collections so far examined there is also a short, broad form, almost square when flattened, and similar to *W. welwitschii*. These may be distinguished as *W. lingulata* by the nearly equilaterally triangular reproductive pouch and the stipe scar near the lateral margin. None of these forms has been observed in flower.

The only published report of flowering is that of Mason (1938) in which he also describes the fruit, seed germination, and seedlings. This species has also been collected in fruit (Daubs 616, 618) in Lake Patzcuaro and in a roadside ditch near Jiquilpan, both in Michoacan, Mexico. As is typical of the genus, the flowers and fruits add little of specific value.

17. WOLFFIELLA GLADIATA (Hegelm.) Hegelmaier

Plate 14

Wolffia gladiata Hegelm. in Lemnac. 133. 1868.

Wolffiella gladiata (Hegelm.) Hegelm. in Bot. Jb. (Engler) 21: 304. 1896.

Plants usually cohering in large numbers, forming dense masses below the surface of the water with only the base of the plant exposed; single plants 4.5–8.0 mm. long, 1.0–2.0 mm. wide at the base, somewhat falcate, tapering from the broad base to a rounded apex; moderate punctate with brown pigment cells in the epidermis; air spaces throughout the basal three-fourths of the plant; reproductive pouch isosceles-triangular in outline, the sides only slightly longer than the base, and the pouch therefore appearing much more nearly equilateral than in *W. floridana*; stipe with a cluster of pigmented cells at the tip located at one corner of the pouch.

Flowers and fruit unknown.

Type locality: Mexico, "near the capital." This species as well as several others collected by Ludwig Hahn bear the notation as shown. This doubtless refers to Mexico, Distrito Federal, and the likely place of collection is the Floating Gardens at Xochimilco. Hahn was a music teacher who spent many years in Mexico and his collections of Lemnaceae, sent to Hegelmaier, served the latter as source material for many of his descriptions, and included the type collections of *W. gladiata* and *W. lingulata*.

Type collection: Hahn (MO, F). Date unknown but described by Hegelmaier in 1868. Type collection examined.

Distribution: Mexico; Argentina; Louisiana.

Collections examined: ARGENTINA: Kurtz (MO), Gruner 537 (UC); LOUISIANA: Reese 1447 (FSU), Daubs 779, 780, 783, 787, 789, 906, 908, 909, 911 (ILL); MEXICO: Daubs 603, 604 (ILL), Hahn (US, MO), Parry (MO), Pringle 7301 (FSU, F), Rose & Hough 4547 (US).

The special problems of identification of this species are discussed under the treatment of *W. oblonga* and *W. floridana*.

No reason is ascribable for the nonflowering of this species. It will doubtless eventually be found in flower, although it is probable that the floral structure will add little in the way of specific characters.

18. WOLFFIELLA FLORIDANA (J. D. Smith) Thompson

Plate 14

Wolffia gladiata var. *floridana* J. D. Smith in Bull. Torrey bot. Cl. 7: 64. 1880.
Wolffiella floridana (J. D. Smith) Thomp. in Rep. Mo. Bot. Gard. 9: 37. 1898.

Plants cohering in large numbers and forming dense masses, floating below the surface of the water or with only the base emersed; single plants usually 5–9 mm. long, occasionally longer, 0.4–0.7 mm. wide, up to 0.5 mm. thick, falcate to doubly curved, attenuate; apex sharply acuminate, base thicker in proportion to width than observed in other members of the genus; moderately punctate on both surfaces with brown pigment cells; air spaces extending through approximately nine-tenths of

the length of the frond; reproductive pouch isosceles-triangular in outline with the sides much longer than the base, stipe at one corner of the pouch.

Flowering cavity either right or left of the median line, opening on the upper surface, flowers and fruit as described for the genus; stomata numerous in emersed portion of flowering frond, rare or lacking otherwise. The flowering frond is much shorter in length and thicker at the base with a larger emersed area than the vegetative plants. It also breaks loose from the usual tangled mass of connected plants and seldom has more than a single young plant attached. (See C of Plate 14.)

Type locality: Florida; Cedar Keys, Levy County.

Type collection: Smith & Austin (MO) or Smith (MO, US, F). Both collections examined.

Distribution: Abundant in inland waters near the Atlantic and Gulf coasts of the United States and common in the Mississippi River valley northward to St. Louis, Missouri.

Collections examined: FLORIDA: Curtis (F, US), Ravenel (MO), Underwood (MO, UC), Smith & Austin (MO), J. D. Smith (MO, US, F), Hook 254 (MO, US, UC, F), Nash (US), Godfrey 54376, 56228, 60607 (FSU), Lemaire 147 (FSU), Hitchcock 2025 (F), Holm (F), Daubs 664, 718, 719, 720, 721, 740, 752, 753, 758 (ILL); GEORGIA: Thorne 4056 (F); ILLINOIS: Swayne (ILL), Seibert 1135 (UC), Hubricht B1946 (MO), Daubs 804, 868, 872 (ILL); INDIANA: Clark 19 (US); LOUISIANA: Reese 1473 (FSU), Fassett 28975 (MO), Daubs 782, 789, 911 (ILL); MISSOURI: Smith 909 (F), Trelease (MO), Widman (MO); MASSACHUSETTS: Blake (US); OHIO: Hicks (MO), Kellerman 4924 (MO, US); SOUTH CAROLINA: Godfrey & Tryon 721 (MO), Godfrey & Tryon 716 (MO, UC, US), Haesloop & Ahles 26585 (FSU); TEXAS: Joor (MO), Trelease (MO), Ferguson & Long (F); VIRGINIA: Fernald, Long, & Griscom 640 (MO, F, UC, MICH, ILL), Hubricht A2361 (MO), Fernald, Long, & Fogg 5252 (MO, UC); DISTRICT OF COLUMBIA: Blake 10867 (MO); ARKANSAS: Daubs 844 (ILL).

Hegelmaier (1896) questioned the advisability of elevating this taxon to species rank, listing it as a variety of *W. gladiata;* Thompson (1898), nevertheless, gave it full species status, a step which now seems thoroughly justified. *Wolffiella floridana* was first reported as flowering by Kurz and Crowson (1946) and was again collected in flower (Daubs 758) in Leon County, Florida, on May 29, 1961. This species has also flowered on two occasions in greenhouse cultures. *W. gladiata* is yet unknown in flowering condition. There are many similarities between these two species, yet the separation of the two seems complete. I have made a number of collections of each of them, finding them either as pure stands, or mixed, with one or the other predominating. If there were an actual

genetic intergradation it would seem that the two forms would always appear mixed and in association with each other. While the extreme forms of each tend to approach each other, a situation fairly common throughout the genus, the constant morphological dissimilarities are marked and justify species separation. The extremely long narrow doubly falcate frond with its much narrower, thicker base; the greater extent of the air spaces; somewhat fewer and larger punctations; and the known flowering condition all serve to separate *W. floridana* from *W. gladiata.*

19. WOLFFIELLA DENTICULATA (Hegelm.) Hegelmaier

Plate 17

Wolffia denticulata Hegelm. in Lemnac. 133. 1868.
Wolffiella denticulata (Hegelm.) in Bot. Jb. (Engler) 21: 305. 1896.

Plants solitary or 2–3 remaining connected; individual plants 4.5–7.0 mm. long by 0.4–0.7 mm. wide; of uniform width or only slightly tapered from base to apex; apex denticulate; sparsely pigmented as compared to other members of the genus; air spaces prominent throughout the length of the frond; reproductive pouch triangular; the stipe much elongated, forming an appendage, pigmented and prominent.

Flowers and fruit unknown.

Type locality: South Africa.

Type collection: Krauss, cited by Hegelmaier.

Distribution: South Africa, known only from this single collection from this area.

Collections examined: The type collection, or a part of it, is in the Herbarium of the Missouri Botanical Garden and has been examined.

This species resembles *W. floridana* in its general morphology but may be distinguished from it through its more uniform width, elongated stipe, and denticulate apex. Hegelmaier apparently knew no more about this species than the meager data supplied by the herbarium label, all of which are presented here. The collection is mixed with *Lemna minor.*

20. WOLFFIELLA OBLONGA (Phil.) Hegelmaier

Plate 16

Lemna oblonga Phil. in Linnaea 29: 45. 1857.
Wolffia oblonga (Phil.) Hegelm. in Lemnac. 131. 1868.
Wolffiella oblonga (Phil.) Hegelm. in Bot. Jb. (Engler) 21: 303. 1896.

Plants solitary or only parent and offspring fronds remaining connected, seldom 3 or more; usually floating just beneath the surface of the water with only a small basal area emersed; single plants 2.0–5.0 mm. long, 0.5–1.5 mm. wide, flat, slightly falcate, base oblique, apex bluntly rounded; punctate on both surfaces with brown pigment cells; air spaces usually extending for only two-thirds the length of the frond; reproductive

pouch isosceles-triangular in outline but with the sides only slightly longer than the basal opening.

Flowering cavity right or left of the median line, opening on the upper surface; flowers and fruit typical of the genus; numerous stomata on the vegetative as well as the flowering frond.

Type locality: Chile, near Santiago. According to Philippi's report "in stagno quodam urbis ipsius Santiago inveni."

Type collection: Philippi, according to Hegelmaier. A collection by Philippi (MO) made in May 1857 from the type locality has been examined.

Distribution: Chile, Argentina, Peru, Panama; Central America, Mexico; Louisiana, Florida.

Collections examined: ARGENTINA: Kurtz 6991A (MO), Pastore 556 (UC), Krapovickas 28792 (F), Lorenz and Hieronymus (MO); CHILE: Philippi (in 1857) (MO); URUGUAY: Herter 150 (MO), Herter, no number but same collection date as previous (MO, F, UC); MEXICO: Schaffner 621 (US); PERU: Killip & Smith 21509 (US); PANAMA: Bartlett & Lasser 16979 (MICH); FLORIDA: Daubs 719, 720 (ILL); LOUISIANA: Daubs 780, 782 (ILL).

Wolffiella oblonga has frequently been confused with the shorter individuals of other species, particularly in herbarium specimens where pressing has obscured important identifying characteristics. It may be distinguished from *W. gladiata* by its more nearly uniform width throughout rather than tapering to the apex, and by the tendency of the entire frond to lie flat on or just beneath the water surface. This latter characteristic also separates it from *W. lingulata*, especially when observed in their natural habitat.

Flowers and fruits of this species were described by Giardelli (1935) from material which she collected near Buenos Aires and constitute up to now the only published record. Flowers are also present in the collection of Lorenz and Hieronymus (MO), also from Argentina. As is characteristic of the genus, the flowers and fruits add little of specific value. Giardelli (*loc. cit.*) has reported the pollen as being 11–15 microns in diameter, considerably smaller than that of other members of the genus or family.

Description of Genus *Wolffia*

Horkelia Reichb. ex Bartl. in Ord. Nat. 76. 1830. Homonym.
Wolffia Horkel ex Schleid. in Linnaea 13: 389. 1839.
Grantia Griff. ex Voigt in Hort. Suburb. Calc. 692. 1845. Notul. 3: 223. 1851.
Bruniera Franch. in Billotia 1:25. 1864.

Tiny floating rootless plants, seldom exceeding 1 mm. in any dimension, scarcely visible as individuals but frequently numerous enough to form a

solid cover on the surface of the water. Plants globose to ovoid, sometimes flattened above, seldom more than 2 remaining connected. A single reproductive pouch at the basal end of the plant, funnel-shaped with a circular opening. Plants loosely cellular, lacking in vascular tissue except for infrequently a few cells in the filament of the stamen. Lacking in anthocyanin pigmentation; a few species punctate with brown pigment cells in the epidermis.

A single flowering cavity opening on the upper surface, on the median line in most species but lateral to it in two; flowers without a spathe, 1 staminate and 1 pistillate flower only, the pistillate always being nearer the base of the frond. Pistillate flower with globular ovary, single orthotropous ovule, short style, circular stigma; staminate flower of a single stamen, one-celled anther opening by a pigmented line of dehiscence across the top, maturing later than the stigma.

Fruit a spherical utricle with persistent style; seed globose or slightly compressed, smooth, with spongy-layered outercoat. Seed appears large in proportion to the frond but seldom exceeds 0.25 mm. in diameter. Operculum prominent.

Eight species of the genus are recognized in this treatise while one, *W. welwitschii*, formerly placed in this genus, has been transferred to *Wolffiella*. The world's smallest flowering plants are found here and the ultimate in reduction in both size and differentiation seems to have been achieved. The genus is of definite tropical or subtropical affinity and is represented by some species throughout most of this world area.

Although flowering is rare, flowers have been observed in all species recognized except *W. punctata*. As is typical of the family, little in the way of specific distinction is added by them, the only readily observable differences being the lateral location in two species, and the punctate stigma in a few species. Not enough flowers were available to determine if this latter is a constant feature. Similarly the flowers do not readily separate the two genera *Wolffia* and *Wolffiella*, and the distinction must be made on vegetative morphology. The basis for this has been discussed.

Key to Species of *Wolffia*

1. Plants punctate on all surfaces with brown pigment cells in epidermis.
    2. Fronds with a prominent conical papilla in center of upper surface. ..... *W. papulifera*
    2′. Fronds with upper surface flat or slightly rounded; no papillae.
        3. Apex of frond obtuse, frond oval in outline, hemispherical beneath. ..... *W. brasiliensis*
        3′. Apex of frond acute, frond elliptical in outline, under surface hemi-ovoid. ..... *W. punctata*

1′. Plants without pigmented cells in epidermis.
4. Fronds with an elongated stipe or other protuberance from lower surface.
5. Protuberance an elongated stipe; flattened, ligamentous.
6. Margin sinuously dentate. . . . . *W. repanda*
6′. Margin entire. . . . . *W. hyalina*
5′. Protuberance a cylindrical parenchymatous extension of the plant body. . . . . *W. microscopica*
4′. Fronds without an elongated stipe.
7. Plants globose, roughened but not flattened on upper surface. . . . . *W. columbiana*
7′. Plants hemispherical below, flattened on the upper surface with a prominent shoulder or rounded margin. . . . . *W. arrhiza*

21. WOLFFIA REPANDA Hegelmaier

Plate 17

Wolffia repanda Hegelm. in Jour. Bot. 3: 113. 1865.

Plants oval in outline, margin sinuously denticulate; flattened on upper surface, with numerous stomata; lower surface moderately arched with small air spaces. Plants 1.0–1.6 mm. in length by 0.7–1.0 mm. wide, and having a much elongated stipe up to 7.5 mm. long and 0.2 mm. wide. This stipe is apparently produced from growth which occurs after the young plant is separated from its parent.

Flower cavity lying to one side of the median line; flowers and fruit characteristic of the genus.

Type locality: Africa: Angola.

Type collection: Welwitsch 205; cited by Hegelmaier.

Distribution: Known only from the type locality and from this single collection.

22. WOLFFIA HYALINA (Delile) Hegelmaier

Plate 17

Lemna hyalina Del. in Fl. Egypt 75. 1813.
Wolffia delilii Schleid. in Linnaea 13: 390. 1839.
Wolffia hyalina (Del.) Hegelm. in Lemnac. 128. 1868.

Plants largest of the genus, being from 1.5–1.8 mm. in length and 1.0–1.2 mm. broad. In outline, oval, flattened above but with rounded margins resembling *W. columbiana* in general symmetry. Margin of the reproductive pouch thin and slightly flared. Similar to *W. repanda* in having an elongated stipe, this being broader and shorter than in the latter species, up to 2.5 mm. long and 0.75 mm. wide. No pigment cells except in line of dehiscence of the anther.

Flower cavity lateral to the median line; flowers and fruit typical of the genus.

Type locality: Egypt, near Cairo.

Type collection: Uncertain; Ehrenberg (MO) from Egypt is cited by Hegelmaier. This specimen examined. The only other specimen I have seen is Sickenberger (MICH), also from Egypt and in flower and fruit.

Distribution: Apparently known only from the Valley of the Nile, principally the delta region.

23. WOLFFIA MICROSCOPICA (Griffith) Kurz

Plate 21

Grantia microscopica Griff. in Notul. 3: 226. 1851.

Wolffia microscopica (Griff.) Kurz in Jour. Linn. Soc. London 9: 265. 1867.

Plants small, frequently approaching the minimum dimensions given, from 0.4–0.9 mm. long by 0.3–0.6 mm. broad, and characterized by the elongate cylindrical protuberance of the ventral surface, not a stipe as in *W. hyalina* or *W. repanda,* but a parenchymatous extension of the plant body and often reaching a length twice that of the dorsal surface. The plants in dorsal view are also distinctive, being elongate-octagonal, dentate at the junction of the almost straight sides of the octagon, the upper surface flat, with many stomata. Air spaces uniformly large throughout. Not punctate except on the line of dehiscence of the anthers and the stigma.

Flowers and fruit characteristic of the genus.

Type locality: India, near Calcutta (Kurz).

Type collection: Griffith (Kurz), location unknown.

Distribution: Apparently limited to India.

Collections examined: Abundant material in flower and fruit supplied by Prof. P. Maheshwari and four collections by Thivy 130, 135, 136, 137, these latter in the Herbarium of the University of Michigan.

This species flowers regularly and was used by Maheshwari (1954, 1956a) for studies in cytology and embryology in the genus. (See Plate 21.)

24. WOLFFIA BRASILIENSIS Weddell

Plate 20

Wolffia brasiliensis Wedd. in Ann. Sci. Nat. III, 12: 170. 1849.

Plants obovoid, apex obtuse, flat or weakly arched above, strongly arched or bellied below. All surfaces are intensely punctate with brown pigment cells; also stigma and anther. Fronds mostly 0.8–1.2 mm. long and 0.5–0.8 mm. broad, 0.3 mm. thick, more densely cellular towards the surface.

Flowers and fruit typical of the genus.

Type locality: Brazil: province of Matto Grosso.

Type collection: Weddell, in July 1845 (MO). Type examined.

Collections examined: BRAZIL: Weddell (MO); MEXICO: Hahn (MO), Daubs 618 (ILL), Pringle 7301 (MICH), Arsene 906 (ILL), Steere 1567 (MICH), Gaumer 570 (MICH); VENEZUELA: Lasser 2004 (MICH).

Distribution: Apparently limited to the area as represented in the collections reported. (See *W. punctata.*)

25. WOLFFIA PUNCTATA Grisebach

Plate 20

Wolffia punctata Griseb. in Fl. Br. West Ind. 512. 1864.

Wolffia brasiliensis var. *borealis* Engelm. ex Hegelm. in Lemnac. 127. 1868.

Plants ellipsoidal, tapering to an acute apex, the upper surface flattened but curving slightly upward to the apex, the under surface ovoid; dorsal surface exposed to the air and containing numerous stomata; air spaces large in lower half of frond, decreasing in size upwardly. Profusely punctate on all surfaces with brown epidermal pigment cells. Plants 0.7–1.2 mm. long, 0.4–0.7 mm. wide.

Flowers and fruit typical of the genus.

Type locality: Jamaica.

Type collection: Wullschlagel, in Trinidad Herbarium.

Distribution: Apparently limited to the West Indies and the North American continent.

Collections examined: UNITED STATES: CALIFORNIA: Mason 14629 (MO, UC); GEORGIA: Thorne 7346 (MO, UC), Thorne 4056 (F); ILLINOIS: Eggert (MO), Hall (F, MO), Patterson (F), Schneck (ILL); INDIANA: Niewland 11331 (MO); KENTUCKY: Alexander 332 (US), McFarland 91 (MICH, MO, UC); MICHIGAN: Daubs 502, 503 (ILL), Grassl 7728 (MICH), Hermann 6979 (MICH, F), Steere 376 (MICH), Hermann 639 (ILL, F, UC); MINNESOTA: Sheldon S6141 (ILL); MISSOURI: Eggert (MICH), Steyermark 20909 (MO), Steyermark 28368 (F); NEBRASKA: Thomson 288 (US); OHIO: Hicks (MO); PENNSYLVANIA: Wahl 15318 (ILL); TENNESSEE: Gattinger (UC); UTAH: Bassett 13812 (MICH), Maguire 2287 (F), Maguire & Muenscher 2286, 2287 (MO); VIRGINIA: Fernald & Long 6788 (MICH, UC), Fernald & Long 12602 (MO), Richmond 749 (ILL, F, MICH), Patterson 610 (FSU); WISCONSIN: Seymore 10834 (ILL), Wadmond (ILL).

CANADA: ONTARIO: Dore 47–1267 (MO), Gillman (MO).

MEXICO: Pringle 7300 (F, UC), Daubs 616 (ILL).

CUBA: Baker (MICH).

Wolffia punctata has frequently been considered synonymous with

W. brasiliensis. Engelmann proposed it as a variety (see above) of the latter, but Thompson (1898) considered it as a valid species. The species are certainly closely allied and particularly difficult to separate in herbarium specimens. The shape of the apex, obtuse in *W. brasiliensis*, and acute and upturned in *W. punctata*, is the most obvious distinguishing feature. Thompson described *W. punctata* as being less punctate but this seems to be true only of the younger plants; this species seems to be somewhat slower to develop the brown pigment cells.

It is strange that Hegelmaier never referred to Grisebach's binomial either in his monograph of 1868 or his revision in 1896, although it is most unlikely that he could have been unaware of it. That he considered the "nordamerikanischen Formen" different is evident both from his descriptions and his reference to Engelmann's varietal epithet.

There is not a clear cut line of demarcation in the distribution of these two species, although I have not recognized any *W. brasiliensis* in the United States. *W. papulifera*, whose range overlaps that of these two species, may also be mistaken for either of them when it has only a weakly developed papilla, and this may further complicate the problem of identification.

26. WOLFFIA PAPULIFERA Thompson

Plate 19

Wolffia papulifera Thomp. in Rep. Mo. Bot. Gard. 9: 40. 1898.

Plants broadly ovate in horizontal outline, apex rounded, margin minutely denticulate, upper surface flat at margin but rising to a prominent conical papilla near the center, under surface ovoid, air spaces prominent in the lower half. Plants 0.6–1.5 mm. long, 0.3–1.0 mm. broad; abundantly punctate on all surfaces, but less so than its related species. Stomata numerous on the exposed upper surface.

Flowers and fruit typical of the genus.

Type locality: Missouri: Columbia.

Type collection: Thompson 250 (MO). Type examined.

Distribution: Eastern and southern United States; Mexico; Argentina.

Collections examined: UNITED STATES: FLORIDA: Daubs 758 (ILL), Godfrey 57680 (US, FSU), Godfrey 59318, 59411 (FSU), Godfrey 56543a (FSU, UC); ILLINOIS: Daubs 545, 863, 869 (ILL), Hubricht B696 (MO), Ownbey (MO), Schneck (ILL); KANSAS: Hitchcock 1136 (MO, MICH); LOUISIANA: Daubs 783, 913, 915, 863, 908, 909 (ILL), Reese 6809 (FSU); MARYLAND: Hermann 11725 (MICH); MISSOURI: Bush (MO), Steyermark 5156, 15208, 23238, 19314, 12073 (MO), Thompson 250 (MO), Wheeler 4744 (ILL, MICH, US).

MEXICO: Daubs 619 (ILL), Pringle (UC).

SOUTH AMERICA: ARGENTINA: Petersen 3115 (US, MO).

27. WOLFFIA COLUMBIANA Karsten

Plate 18

Wolffia columbiana Karst. in Bot. Unters. 1: 103. 1865.

Fronds ellipsoid to spheroid, symmetrical, only the upper surface above the water, this exposed area slightly roughened and containing a few (1–6) stomata. Plants 0.8–1.4 mm. long by 0.4–0.8 mm. broad, loosely cellular, with large air spaces throughout; neither pigmented nor punctate except for the line of dehiscence of the anthers.

Flowering pouch on the median line; flowers and fruit characteristic of the genus.

Type locality: South America: Colombia.

Type collection: Karsten; his description includes mention also of collections from Venezuela. Type collection not seen, but specimens from type locality examined.

Distribution: Except for Colombia and Venezuela in South America, exclusively in Central and North America.

Collections examined: UNITED STATES: ARKANSAS: Daubs 830, 838 (ILL); CALIFORNIA: Mason 12864 (MICH, UC); CONNECTICUT: Fernald 173 (MICH, MO); DISTRICT OF COLUMBIA: Blake 10868 (MO); FLORIDA: Daubs 752, 775, 879, 671 (ILL), Godfrey 60607 (FSU), Godfrey 57680 (MO); ILLINOIS: Daubs 803, 804, 860, 872 (ILL), Hall (MO), Eggert (MO), V. H. Chase 13316, 11664 (ILL), G. N. Jones 1669, 15226, 16580 (ILL), Evers 1500 (ILL); INDIANA: Daubs 501 (ILL), Ahles 3428 (ILL), Hill (ILL), Umbach (MO); IOWA: Shimek (MO); KANSAS: Hitchcock 1137 (MO); LOUISIANA: Daubs 788, 793, 778, 906, 909 (ILL), Reese 5809 (FSU); MASSACHUSETTS: Torrey (FSU); MICHIGAN: Ehlers 1851 (ILL), Hermann 6979 (MICH, F, US, MO), Gillman (MO), Grassl 7274 (MICH), Voss 9671 (MICH); MINNESOTA: Moore 13598, 21134 (UC), Moore & Huff 18469 (ILL); MISSOURI: Steyermark 23238 (UC, F), Eggert (MO), Engelmann (MO), Bush 524 (MO); NEW YORK: Randolph & Wiegand 9553 (F), Wiegand 15044 (MO), Muenscher & Maguire 2116 (MO), Austin (MO), Clausen 2658 (UC); OHIO: Hicks (MO), Leonard 6653 (US); OKLAHOMA: Stevens 1883 (MO); PENNSYLVANIA: Benner 7452 (MO), Benner 3867 (MICH), Glowenke 11476 (ILL, UC); SOUTH CAROLINA: Ravenel (MO); TENNESSEE: Gattinger (F); TEXAS: Barkley 13116 (FSU, UC, F, MO); VIRGINIA: Fernald & Long 6788 (F); WISCONSIN: Wadmond (ILL), Fassett & Wilson 5104 (MICH).

CANADA: ONTARIO: Dore 47–1268 (MO), Dore & Gillett 13905 (ILL, MICH), Gillman (MO), Shields 433, 433a (MO).

MEXICO: Hahn (MO), Daubs 635, 616, 619 (ILL), Arsene 57 (F), Arsene 906 (MO), Fassett 28474 (MO), Steere 1566 (MICH), Gaumer 570 (MO, US, F).

EL SALVADOR: Fassett 28688, 28558 (F).

GUATEMALA: Kellerman 6630 (F).

SOUTH AMERICA: COLOMBIA: Gutierrez & Barkley 18C–005, 18C–006 (F), Molina & Barkley 19BO–205 (US); CURACAO: Britton & Shafer 2994 (US).

This species seems to be the New World counterpart of *W. arrhiza*, but is easily distinguished from that species by the large air spaces throughout the frond, by its rounded, slightly roughened surface, and by the lack of any prominent edge or "shoulders" differentiating the sides from the top.

According to Hegelmaier (1868) this species had been reported from the United States some time before Karsten's description of it from South America. He specifically cites *Robbins*: Connecticut in 1829, and *Riddell*: Louisiana in 1840. In view of its wide distribution in the United States and Mexico and rather limited occurrence in South America, this is not surprising.

28. WOLFFIA ARRHIZA (L.) Wimmer

Plate 18

Lemna arrhiza L. in Mant. 294. 1766.
Lenticula arrhiza Lam. in Fl. Fr. 2: 190. 1778.
Lemna globosa Roxb. in Fl. Ind. 3: 565. 1832.
Lemna arrhiza Willd. ex Schleid. in Linnaea 13: 390. 1839.
Wolffia michelii Schleid. in Beiträge Bot. 233. 1844.
Grantia globosa Griff. in Notul. 3: 229. 1851.
Wolffia arrhiza (L.) Wimm. in Fl. Schles. 140. 1857.
Bruniera vivipara Franch. in Billotia 1: 25. 1864.
Wolffia delilii Kurz (non Schleiden, 1839) in Jour. Linn. Soc. London 9: 265. 1867.
Wolffia cylindracea Hegelm. in Lemnac. 123. 1868.

Plants ellipsoidal, the upper surface weakly arched or convex, with a strongly delimited, rounded border or shoulder; dorsal surface strongly bellied. Numerous stomata on the exposed surface; no pigmented or punctate cells except in the anther. Plants often quite small, 0.5–1.2 mm. long, 0.4–1.0 mm. wide, more frequently approaching the lower range in size. Lower half of frond loosely cellular with large air spaces, the upper more dense and the air spaces smaller.

Flowers and fruit characteristic of the genus.

Type locality: Europe: Italy.

Type collection: Not listed by Savage (1945).

Distribution: Europe; India, Japan, Philippines; not known in the Western Hemisphere.

Collections examined: BOHEMIA: Podpera (MO); FRANCE: Casson (MO), Nerpaut (US), Chassagne (US); HUNGARY: Topa (MO), Karpati

(FSU); GERMANY: Ludwig (MO), A. Braun (?) (MO); INDIA: Thivy 127, 138 (MICH); ITALY: Ball (US), Mori 8114 (UC); JAPAN: Ito 1229 (US, UC); NETHERLANDS: Florschutz (MO); POLAND: Raciborski (MO); PHILIPPINES: E. D. Merrill 4244 (US). Living specimens supplied by William S. Hillman of Yale University were also examined.

Wolffia arrhiza would appear to be allied with *W. columbiana* in its lack of any pigmentation or significant punctation, but is clearly differentiated morphologically, and separated geographically, so that there is little reason for any confusion in identification. Mason (1957) has reported *W. arrhiza* from California but I have examined his collection and find his species to be *W. punctata*. Also his statement "world-wide in temperate zones" is too inclusive, as this species is still unconfirmed in the Western Hemisphere.

The binomial *Wolffia cylindracea* is used by Hegelmaier (1868, 1895), although categorized as another of his "zweifelhafte" species. Inasmuch as many individuals of *W. arrhiza* quite accurately conform to Hegelmaier's drawings and descriptions of *W. cylindracea*, I have placed this latter binomial in synonymy.

IV. TABLES OF COMPARISONS OF SPECIES

TABLE I

COMPARISON OF SPECIES OF SPIRODELA

		intermedia	*polyrhiza*	*polyrhiza* var. *masonii*	*biperforata*	*oligorhiza*	*punctata*
Number cohering		3–5	2–5	2–5	2–5	2–5	3–5
Size in mm.	Length	5.0–10.0	3.0–10.0	3.0–8.0	5.0–6.5	2.5–5.0	2.0–3.5
	Width	4.0–8.0	2.5–8.0	2.5–6.0	3.5–5.0	1.2–3.0	1.2–2.0
Shape	Outline	orbicular to elliptical	orbicular to obovate	orbicular to obovate	elongate-elliptical	elliptical-obovate to reniform	elliptical to reniform
	Apex	obtuse	obtuse	obtuse	obtuse	obtuse to acute	acute
	Base	asymmetrical	asymmetrical	asymmetrical	strongly asymmetrical	elongate, acute	acute
Pigmentation		strongly red-purple pigmented			moderate	strongly so	moderate
Upper surface		flattened	flattened	flattened	flat	flat-convex	convex
Lower surface		strongly convex, inflated	flat to slightly convex	strongly convex, inflated	flat	convex, slightly inflated	convex
Nervature		7–10 obscure	5–12 prominent	5–10 perceptible	10–12 perceptible	3-5 obscure	3 obscure
Number of roots		10–18	5–12	5–12	5–10	2–5	1–3
Number of roots penetrating prophyllum		3–4	1	1	2	—	—
Fruit	Ovule position	anatropous	amphitropous or anatropous	fruit unknown	anatropous	amphitropous	amphitropous
	Number of seeds	4	1–2		2	1	1
Turions formed		no	yes	yes	no	no	no
Cell inclusions		all species rich in raphides and druses					

COMPARISON OF SPECIES OF LEMNA

		gibba	*disperma*	*obscura*	*minor*	*perpusilla*	*trinervis*	*valdiviana*	*minima*	*trisulca*
Number cohering		2–4	1–3	1–3	2–5	2–5	2–4	2–10	1–2	many
Size in mm.	Length	3.5–6.0	1.5–3.5	1.5–3.5	3.0–6.0	1.0–2.5	2.0–5.0	2.5–5.0	1.0–2.5	5.0–20.0
	Width	2.5–5.0	0.9–2.5	1.0–2.5	1.5–4.0	0.7–2.0	1.5–3.0	0.5–1.5	0.5–1.5	2.5–5.0
Shape	Outline	orbicular-obovate	elliptical-obovate	elliptical-obovate	elliptical-orbicular	orbicular-obovate	obovate	elliptical	oval	elongate-lanceolate
	Apex	asymmetrically truncate	obtuse	obtuse	symmetrical, obtuse	obtuse	rounded	obtuse	obtuse	denticulate
	Base	symmetrical, subacute	subacute	subacute	asymmetrical, obtuse	asymmetrical, obtuse	subacute	strongly asymmetrical	symmetrical, obtuse	acute
Color and pigmentation		yellow-green, red-purple on both surfaces	medium green, strongly red-purple below	medium green, strongly red-purple below	dark green, often red-purple below	medium green, not pigmented	light green, not pigmented	light green, not pigmented	medium green, not pigmented	medium green, not pigmented
Conformation of upper surface		slightly convex	slightly convex	slightly convex	flat to slightly convex	convex, prominent papillae	flattened	flattened	flat to slightly convex	flattened
Conformation of lower surface		strongly convex, inflated	convex to slightly inflated	convex to slightly inflated	slightly convex	slightly convex	flat	flat	flat to slightly convex	flat
Root sheath		cylindrical, prominent	short, not prominent	short, not prominent	not prominent	slightly to prominently winged	prominently winged	not prominent	thin, cylindrical	not prominent
Rootcap		long, straight, point obtuse	point usually acute	point obtuse	prominent, obtuse	acute, curved	acute	strongly curved, obtuse	obtuse	acute
Fruit	Shape and position	cordate, winged, flattened, slightly projecting	broad, winged, slightly flattened, ⅓ projecting	ovoid, not winged, ⅓ projecting	obovate, not winged, slightly flattened	ovoid, oblique in pouch	ellipsoid, slightly oblique	ellipsoid, long-exserted	elongate, long-exserted	ovoid, striate, ½ projecting
	Number of seeds	1–6	2	1	1	1	1	1	1	1
	Ovule position	amphitropous-anatropous	amphitropous	amphitropous	amphitropous	obliquely orthotropous	obliquely orthotropous	orthotropous	orthotropous	amphitropous
Seed	Shape	broadly ovoid	obvate, slightly flattened	ovoid	obovoid, slightly flattened	ovoid	elongate-ovoid	ellipsoid	elongate	broadly ovoid
	Surface	unevenly ribbed	ribbed	ribbed	smooth	deeply ribbed	ribbed	ribbed	ribbed	ribbed

TABLE III

COMPARISON OF SPECIES OF WOLFFIELLA

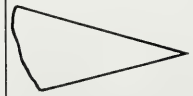
		welwitschii	*lingulata*	*gladiata*	*floridana*	*denticulata*	*oblonga*
Number cohering		solitary or 2–3	solitary or 2–3	many, forming colonies	many, forming colonies	2–5, seldom more	2–3, seldom more
Size in mm.	Length	5.0–6.0	3.5–7.5	4.5–8.0	5.0–9.0	4.5–7.0	2.5–5.0
	Width	3.0–4.0	1.5–4.0	1.0–2.0	0.4–0.7	0.4–0.7	0.5–1.5
Shape or appearance		rectangular, flat, margins curled	attached plants curved, forming an arc	base broad, tapering to obtuse apex	attenuate, falcate, apex acuminate	uniform width, apex denticulate	oblong, slightly curved
Extent of air spaces		basal ⅓ of frond	basal ⅓ to ⅖ of frond	basal ¾ of frond	for 9/10 of length	throughout	basal ⅜ of length
Shape of reproductive pouch in outline							
Number and location of flowering cavities		2, lateral	1, lateral	flowering unknown	1, lateral	flowering unknown	1, lateral

TABLE IV

COMPARISON OF SPECIES OF WOLFFIA

		repanda	*hyalina*	*microscopica*	*brasiliensis*	*punctata*	*papulifera*	*columbiana*	*arrhiza*
Size in mm.	Length	1.0–1.6	1.5–1.8	0.4–0.9	0.8–1.2	0.7–1.2	0.6–1.5	0.8–1.4	0.5–1.2
	Width	0.7–1.0	1.0–1.2	0.3–0.6	0.5–0.8	0.4–0.7	0.3–1.0	0.4–0.8	0.4–1.0
Shape in dorsal view outline		oval, base truncate	round to oval	elongate-octagonal	obovoid, apex obtuse	ovate, apex acute	ovate, apex acute	round to ellipsoid	round to ellipsoid
Upper surface		flat, margins repand	rounded, slightly flattened	flat with dentate margin	weakly arched	flat, rising at apex	conical papilla, center	convex, slightly flattened	flat, rounded shoulders
Lower surface		moderately convex	spherical	elongate-cylindrical	laterally convex	boat-shaped, rising to apex	hemi-ovoid	spherical	hemispherical
Stipe		elongate 0.2×7.5 mm.	elongate 0.75×2.5 mm.	short or sessile	short to sessile	short to sessile	short to sessile	short to sessile	short to sessile
Air spaces		small throughout	large throughout	small, uniform throughout	small above, large below	small above, large below	small above, large below	large throughout	small above, large below
Location of punctate cells		anther	anther	anther and stigma	profusely on all surfaces	profusely on all surfaces	moderate on all surfaces	anthers only	anthers only
Position of flowers		lateral	lateral	median	median	median	median	median	median

PLATES

PLATE 1. Comparison of *Pistia* and *Spirodela*.

A, longitudinal section of inflorescence of *Pistia;* ov, ovule; p, pistil; sp, spathe; st, stamen (× 20); B, schematic diagram of spiral sympodial branching of *Pistia;* pro, prophyllum; 1, leaf; b, bract; inf, inflorescence; sp, spathe; C, sections through pouch of *Spirodela* showing developing young plant, the lower section is the older; pp, parent plant; pro, prophyllum; yp, young plant; r, root (× 40); D, longitudinal section of tip of young stolon of *Pistia;* r, roots; pro, prophyllum; 1, leaf (× 20).

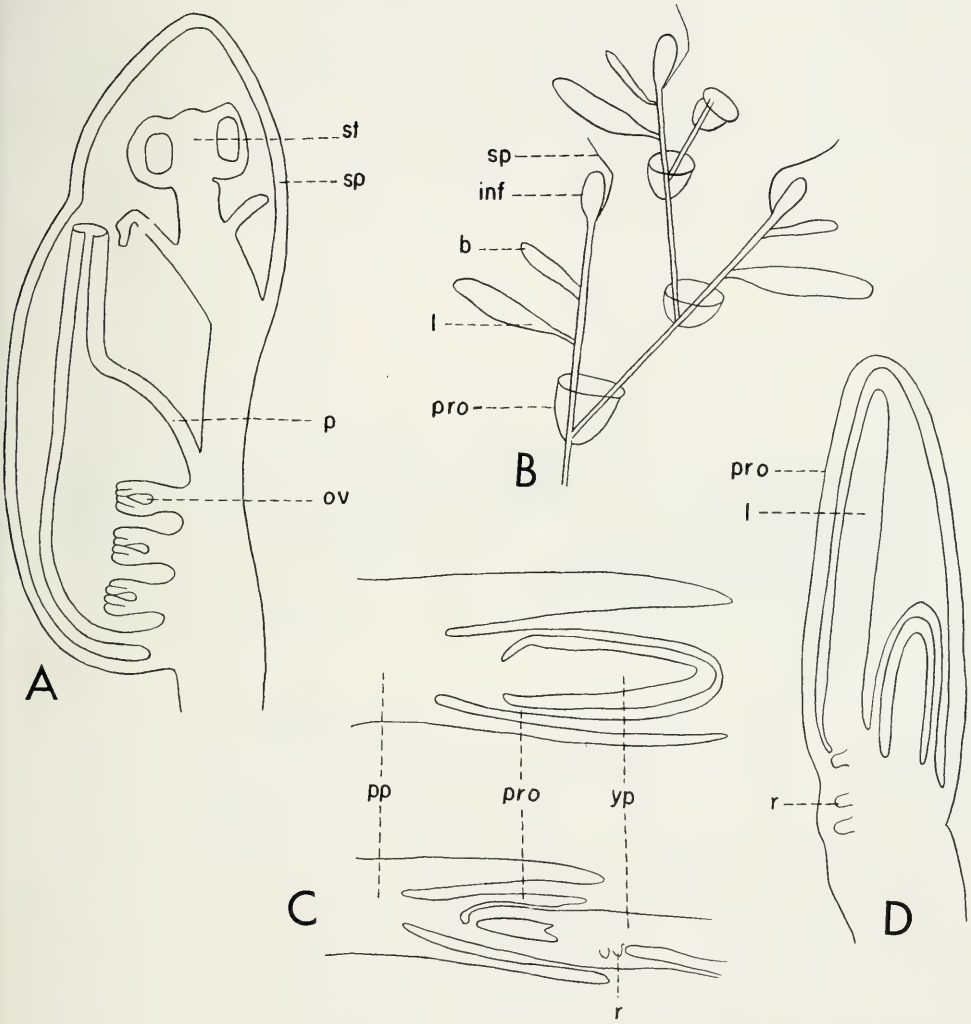

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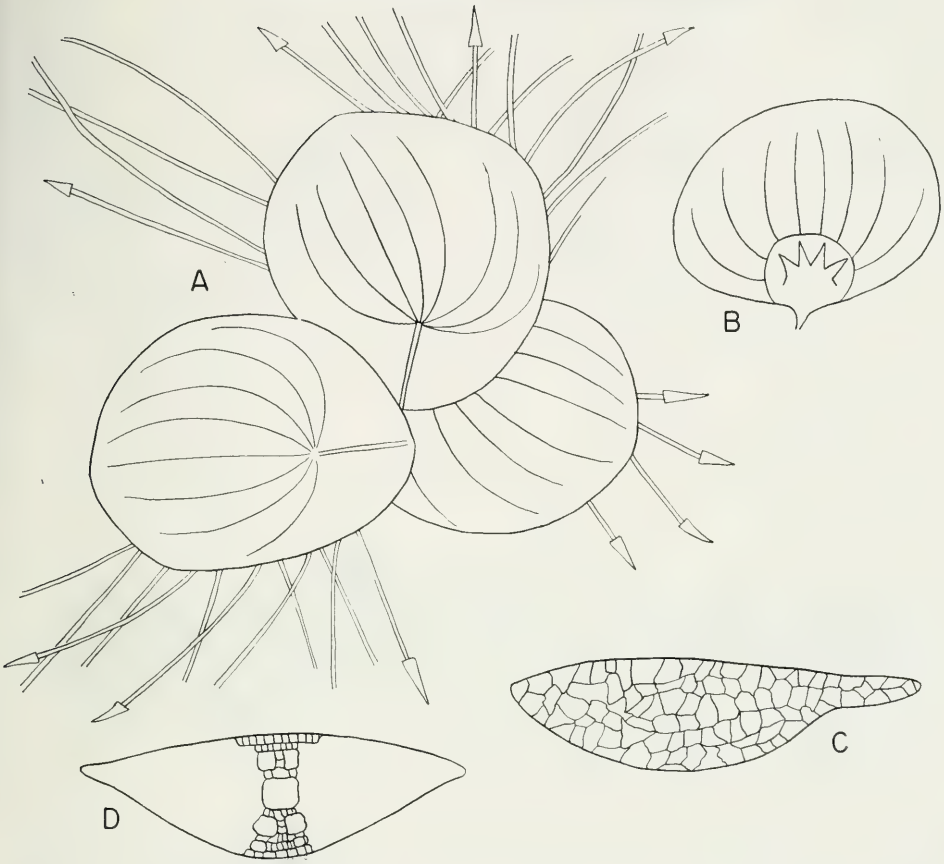
PLATE 2. *Spirodela intermedia.*

A, habit sketch showing shape of plants, nervature, numerous fascicled roots with acute rootcap; B, ventral view of single plant showing first four roots penetrating the prophyllum; C, nearly median longitudinal section, and D, nearly median transverse section, showing convex surfaces and many layers of air spaces; E, distribution. (All drawings × 5.)

Spirodela intermedia



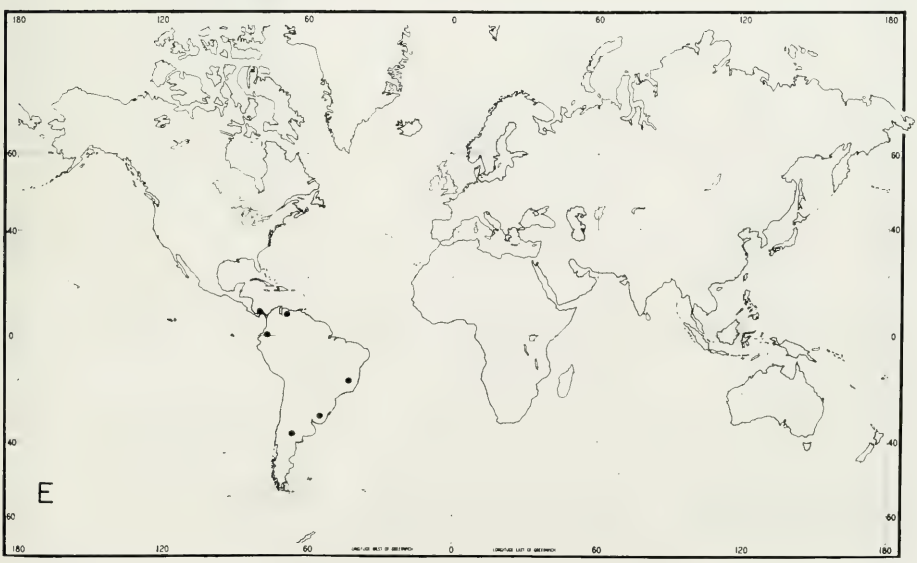


PLATE 3. *Spirodela polyrhiza.*

A, habit sketch of several attached floating plants (× 2.5); B, ventral view showing long connecting stipes and only the first root penetrating the prophyllum (× 2.5); C, root tip with acute rootcap (× 10); D, turion or overwintering bud (× 10); E, median longitudinal section showing the relatively flat surfaces and distribution of air spaces (× 2.5); F, fruit with nearly mature seed; o, operculum; c, chalaza (× 15); G, anatropous position of ovules when two or more are present (× 40); H, distribution.

Spirodela polyrhiza

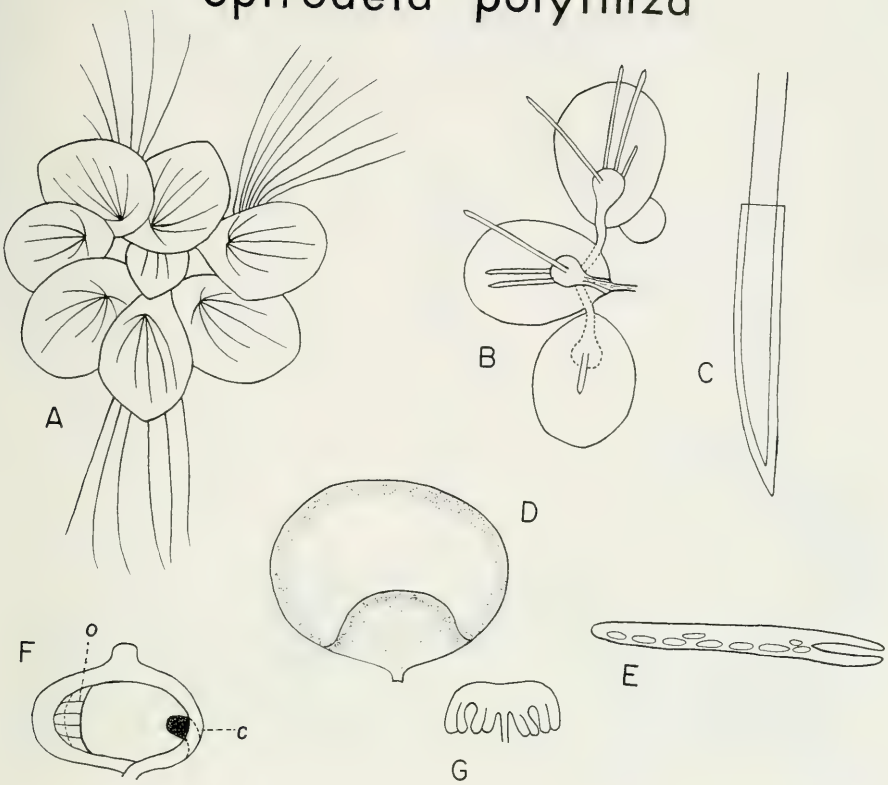
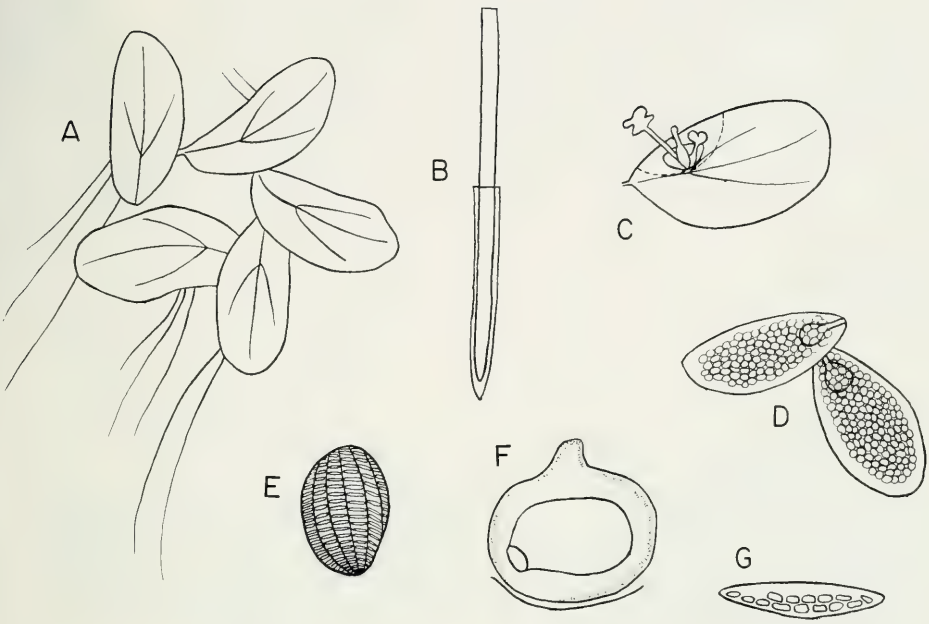


PLATE 4. *Spirodela oligorhiza.*

A, habit sketch of several attached floating plants (× 5); B, root tip with mucronate rootcap (× 10); C, flowering frond with one mature anther (× 12.5); D, ventral view showing prominent air spaces (× 5); E, seed, longitudinally ribbed and transversely striate (× 22.5); F, nearly mature fruit with single seed (× 15); G, median transverse section showing convex surfaces and air spaces (× 5); H, distribution.

Spirodela oligorhiza



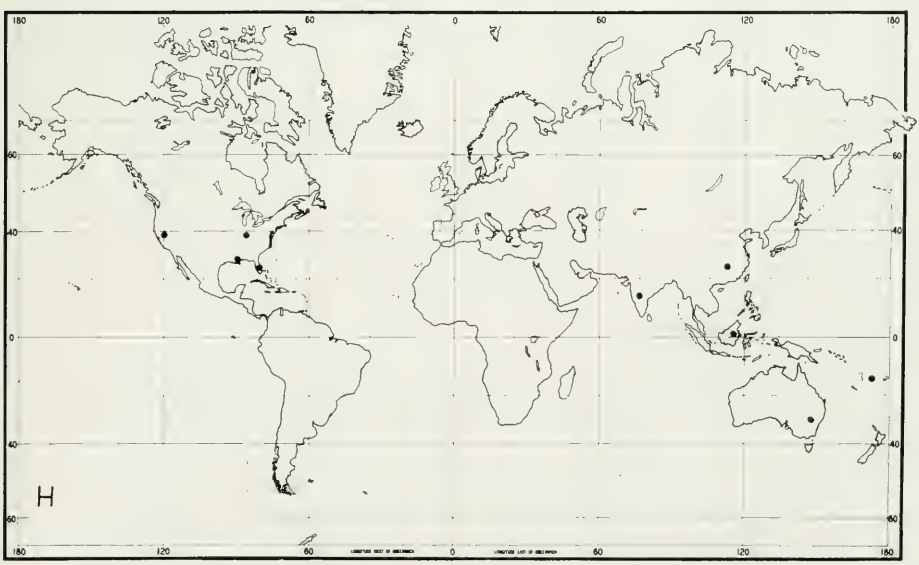


PLATE 5. *Spirodela biperforata.*

A, habit sketch showing the typically asymmetrical plants (× 5); B, root tip with acute rootcap (× 9); C, ventral view showing first two roots penetrating prophyllum (× 5); D, median transverse section showing nearly flat dorsal surface and slightly convex lower surface (× 5); E, cells containing raphides and druses, abundant throughout plant (× 180); F, ventral view showing the uniform size and distribution of air spaces (× 5); G, distribution.

Spirodela biperforata

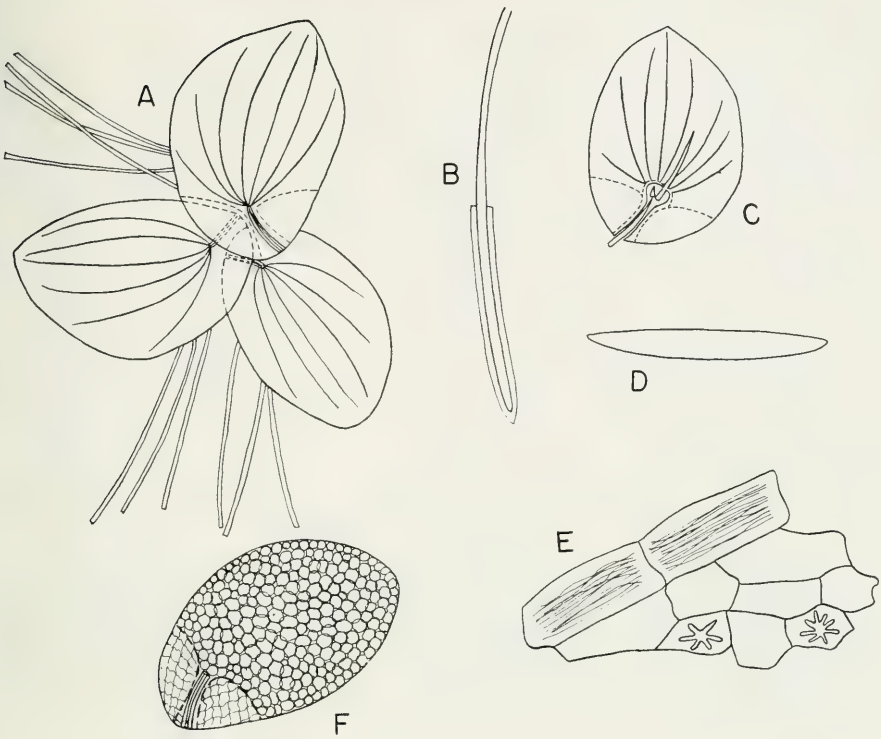


PLATE 6. *Lemna trisulca.*

A, habit sketch of attached vegetative plants showing the elongate stipe, serrate margin, and acute rootcap (× 5); B, flowering plants, usually short-stipitate (× 5); C, germinating seed; r, root; c, cotyledon; f, young frond; o, operculum (× 15); D, distribution. (C, after Hegelmaier.)

Lemna trisulca

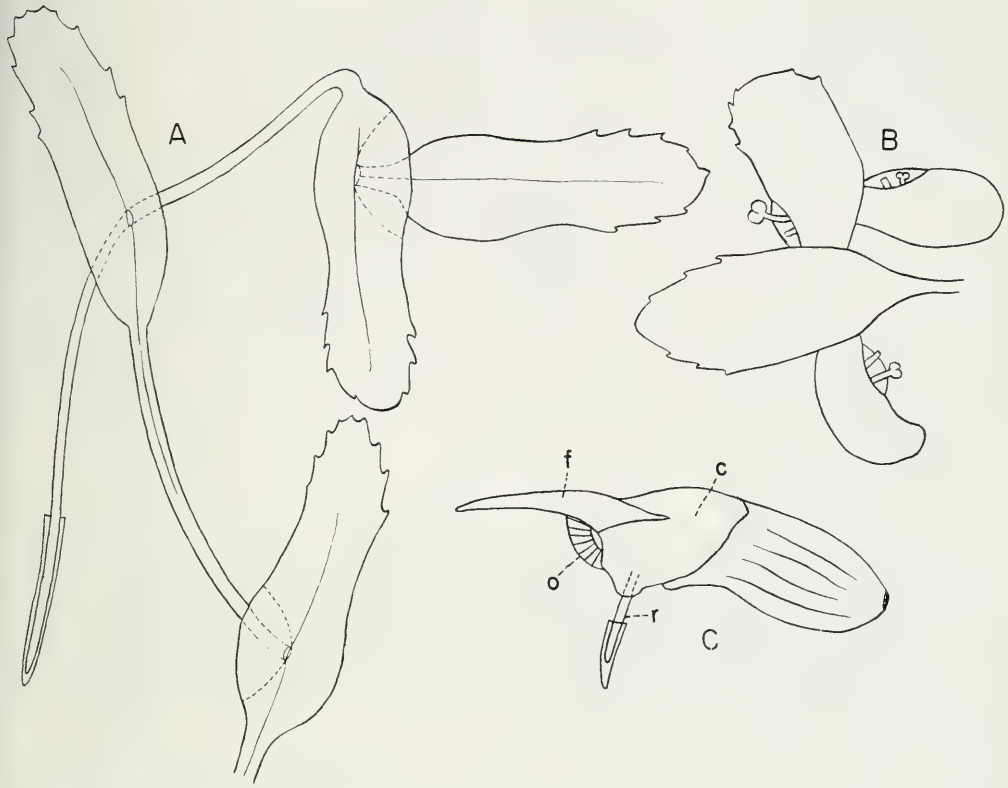
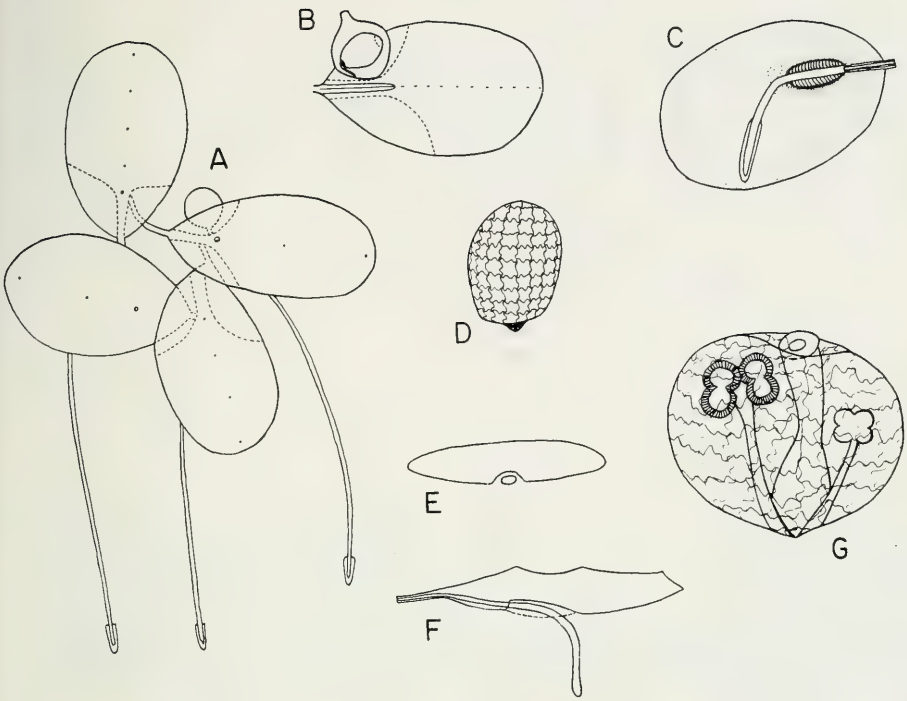


PLATE 7. *Lemna minor.*

A, habit sketch of attached plants showing long roots with obtuse rootcaps (× 5); B, fruiting plant (× 5); C, ventral surface showing young root in furrow (× 5); D, seed with reticulate seed coat (× 20); E, median transverse section, and F, median longitudinal section showing the characteristic slightly convex surfaces and the root furrow (× 5); G, flowers, enclosed in spathe open only at top (× 40); H, distribution.

Lemna minor



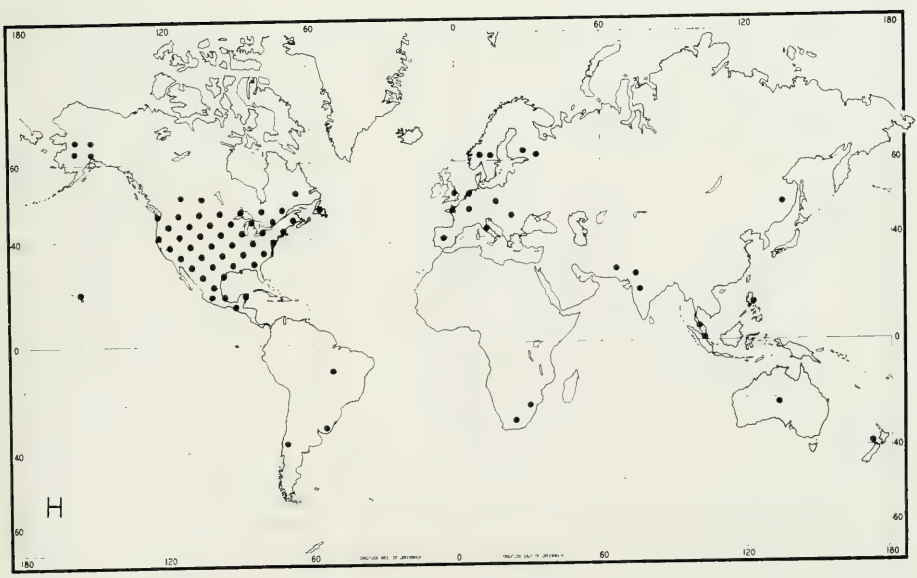
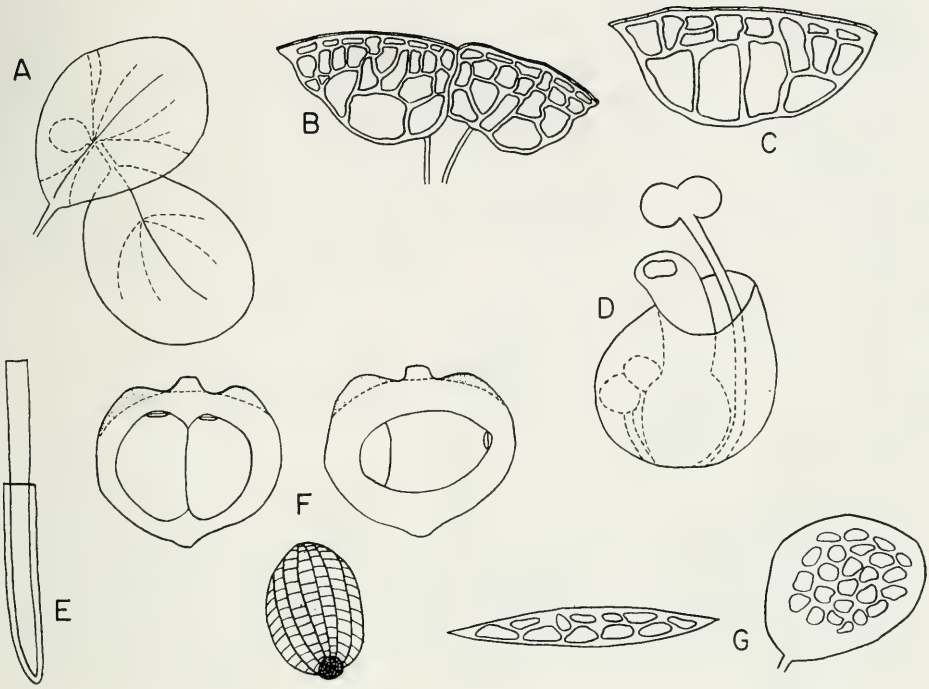


PLATE 8. *Lemna gibba.*

A, dorsal view of mature frond showing large reproductive pouches with young plants in each (× 4); B and C, nearly median longitudinal sections showing greatly inflated air spaces of gibbous plants (× 4); D, typical flowering structure (× 40); E, root tip with obtuse rootcap (× 20); F, one- and two-seeded fruits showing ovule position and winged shoulders, and the ribbed, transversely striate seed (× 17.5); G, median transverse section and ventral surface of nongibbous frond showing the prominent but uninflated air spaces (× 4); H, distribution.

Lemna gibba



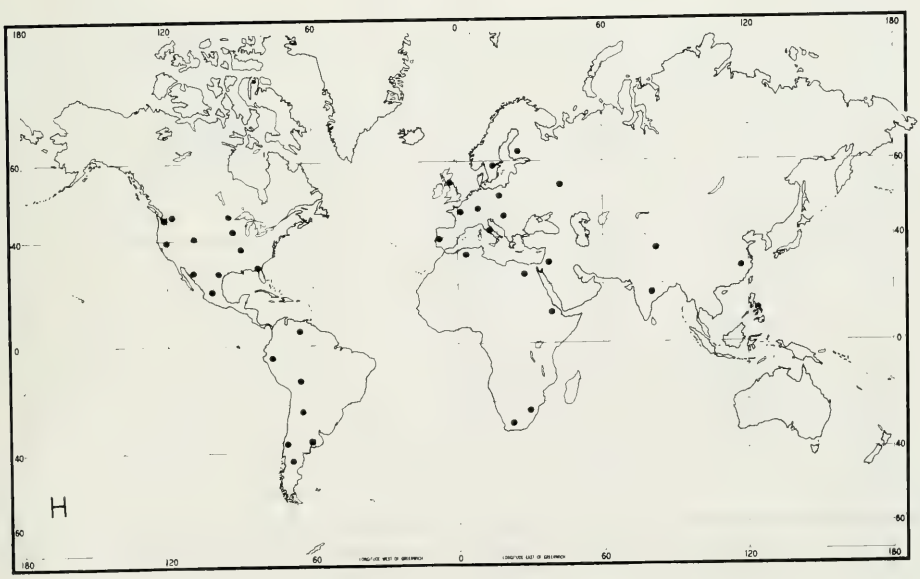
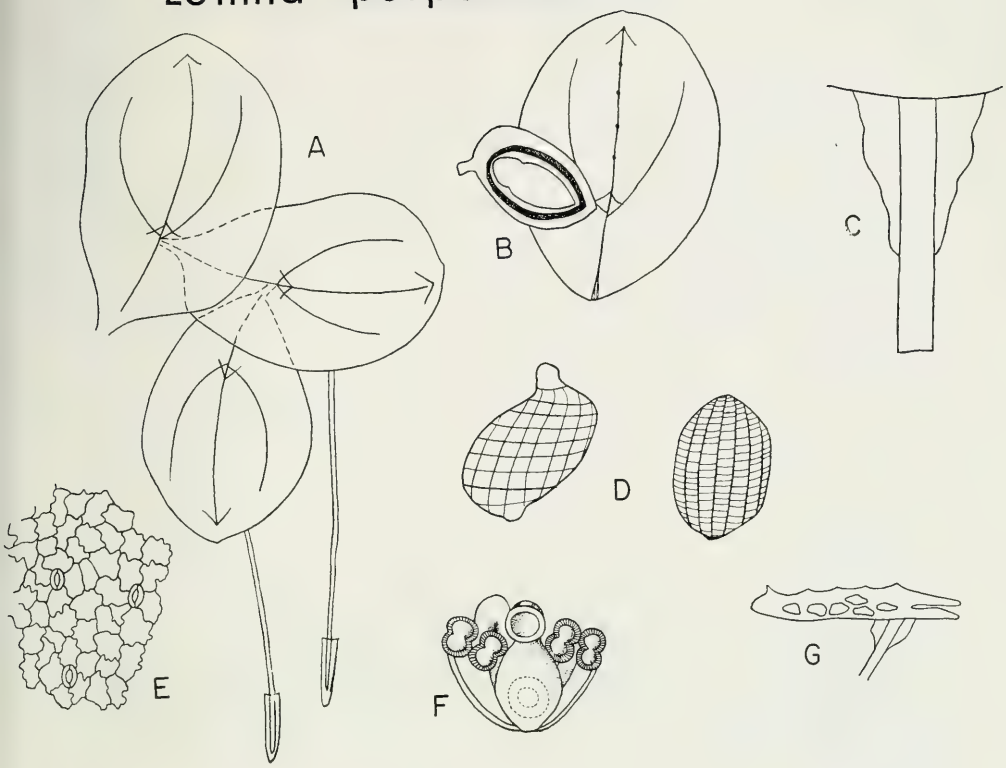


PLATE 9. *Lemna perpusilla.*

A, habit sketch of mature plants (× 7.5); B, fruiting plant showing the oblique fruit position and lateral style (× 10); C, winged root sheath (× 20); D, fruit (left) and seed (× 12.5); E, section of epidermis (× 75); F, typical flowering structure (× 30); G, median longitudinal section showing the thick frond, prominent papillae, and winged root sheath (× 6); H, distribution.

Lemna perpusilla



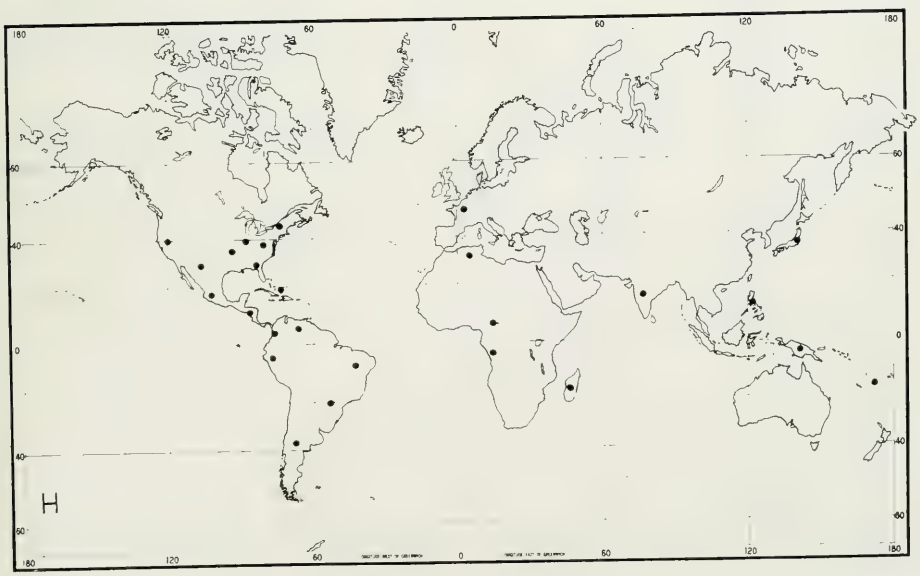
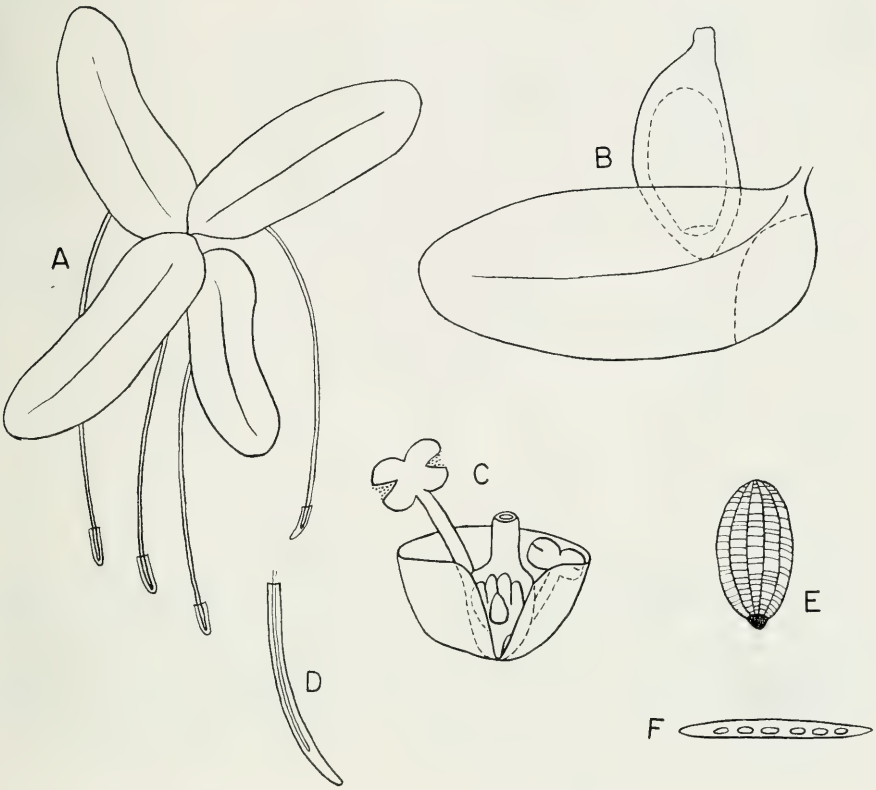


PLATE 10. *Lemna valdiviana.*

A, habit sketch showing characteristic shape of fronds (× 7.5); B, fruiting frond showing the long-exserted fruit and asymmetric base of frond (× 12.5); C, typical flowering structures, also showing orthotropous ovule (× 30); D, sharply curved root tip (× 15); E, seed (× 25); F, median transverse section of thin flat frond, showing air spaces (× 5); G, distribution.

Lemna valdiviana



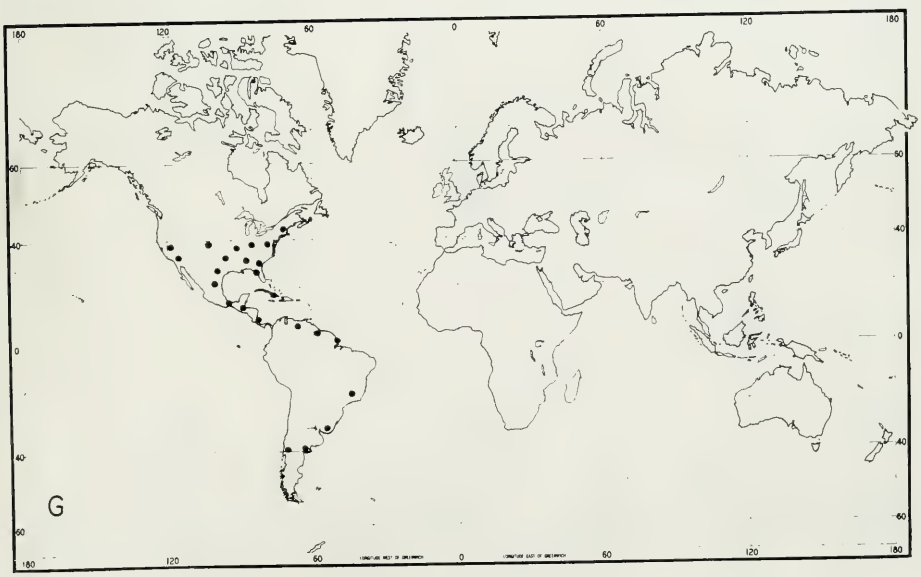
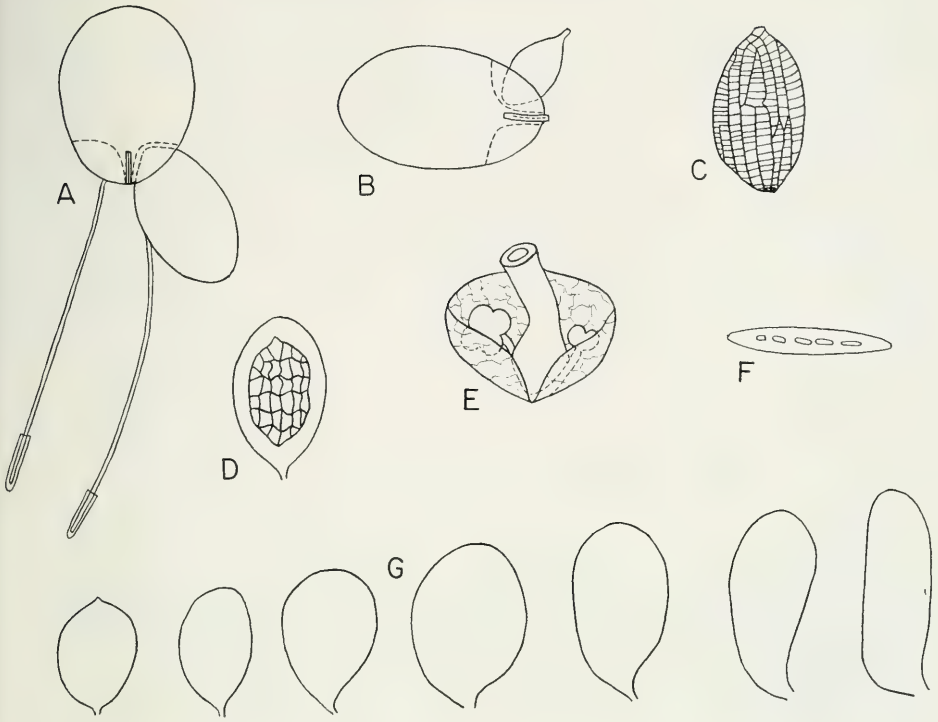


PLATE 11. *Lemna minima.*

A, mature frond of characteristic shape with young frond showing typical attachment (× 7.5); B, fruiting frond showing typical shape and attachment of fruit (× 7.5); C, seed (× 25); D, location of air spaces, causing frond to be thin-margined (× 6); E, flowers, in spathe (× 30); F, median transverse section of frond (× 7.5); G, range in shapes of mature fronds from typical *L. minima* (left) to typical *L. valdiviana* (right) (× 5); H, distribution.

Lemna minima



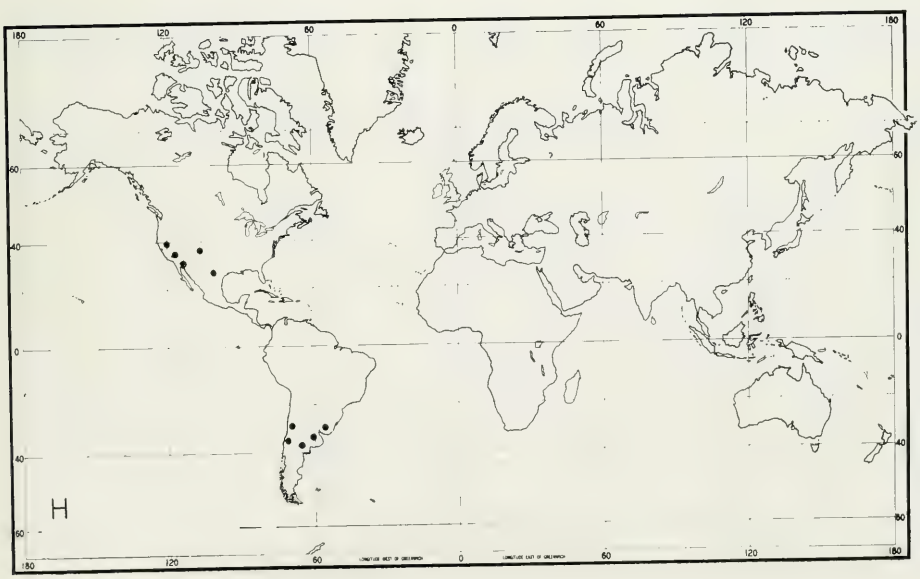


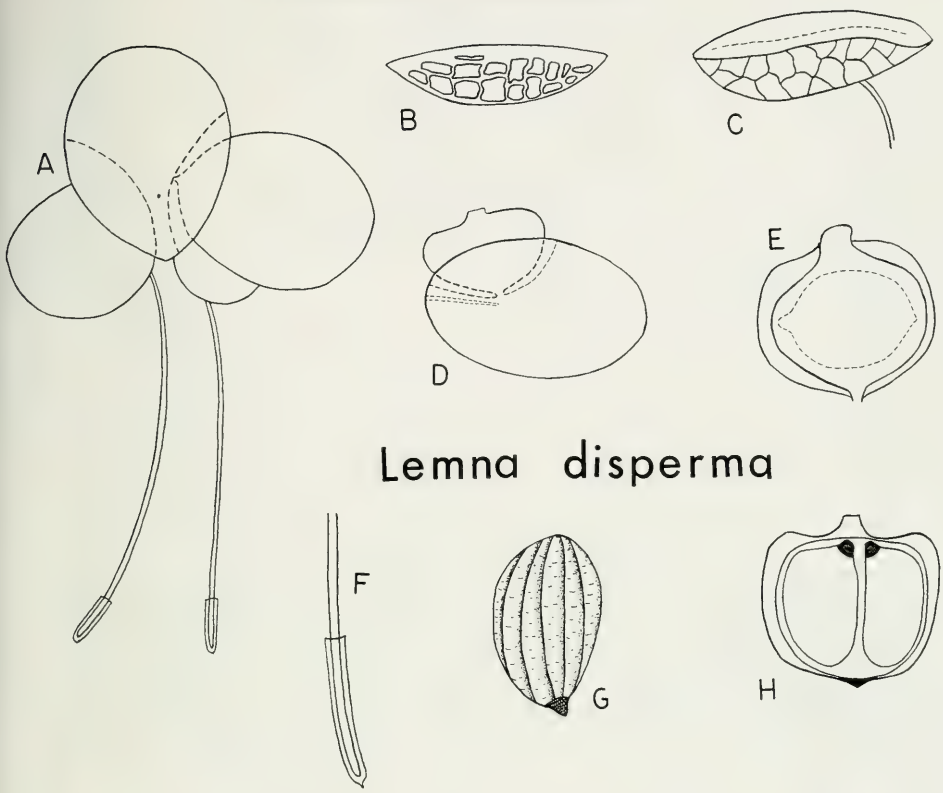
PLATE 12. *Lemna obscura.*

A, habit sketch showing typical shape, elongate reproductive pouches, obtuse rootcap (× 5); B, median transverse section showing the convex surfaces and moderately inflated air spaces (× 7.5); C, lateral view of adult plant (× 7.5); D, fruiting plant (× 5); E, fruit with single seed (× 15).

Lemna disperma. F, mucronate rootcap (× 10); G, seed (× 20); H, fruit, two-seeded (× 17.5).

I, distribution.

Lemna obscura



Lemna disperma

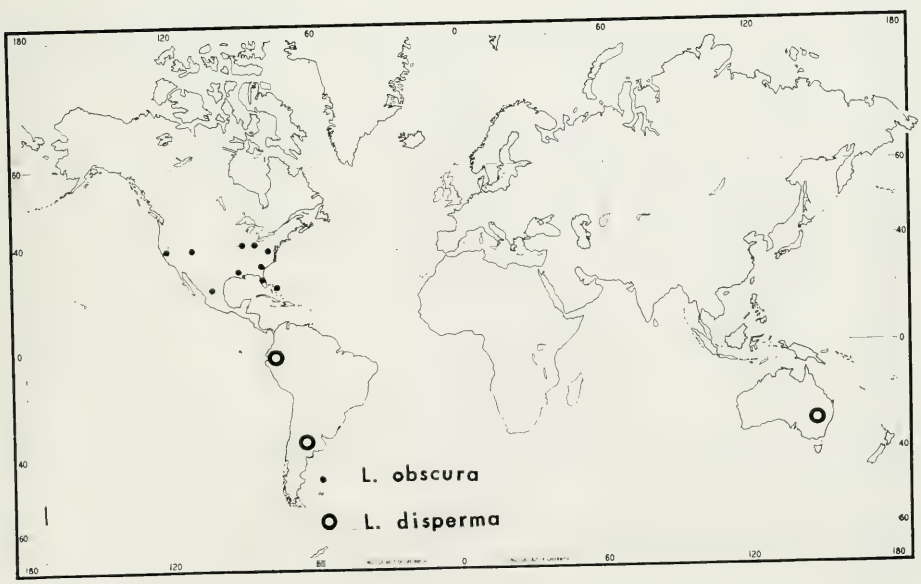
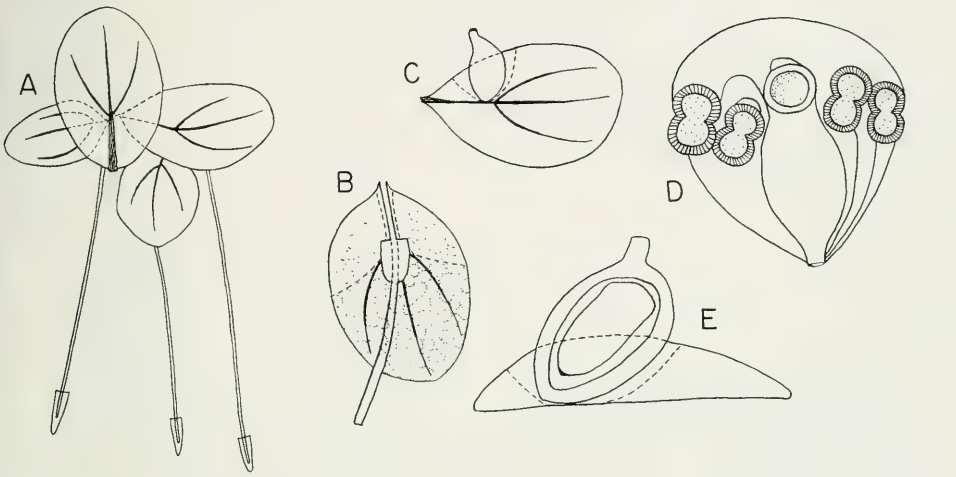


PLATE 13. *Lemna trinervis.*

A, habit sketch of adult and young plants showing the prominent nerves and acute rootcap (× 4); B, ventral view showing winged root sheath and uniform air spaces (× 7.5); C, fruiting plant with immature fruit (× 6); D, typical flowering structures (× 40); E, nearly mature fruit, slightly oblique in pouch (× 17.5); F, distribution.

Lemna trinervis



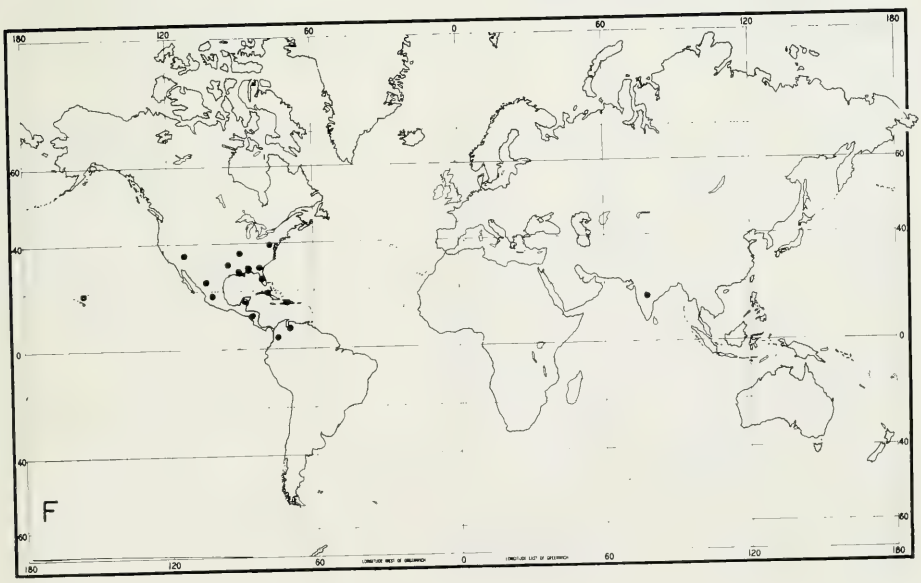


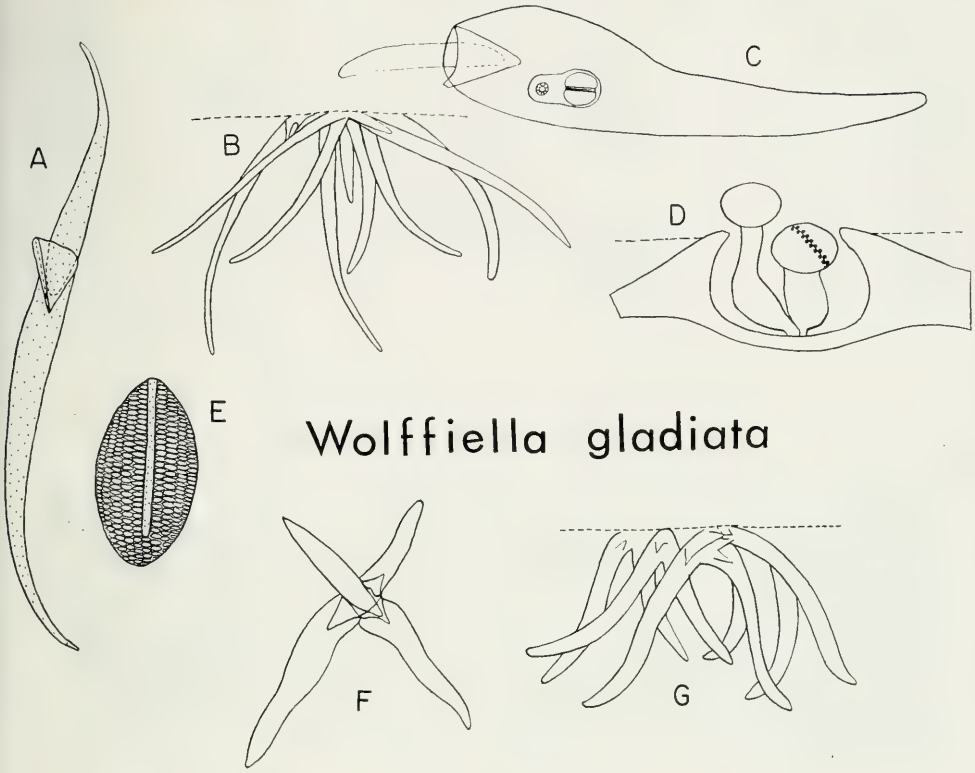
PLATE 14. *Wolffiella floridana.*

A, attached mature and young plants showing typical falcate shape, acuminate apex, and punctate condition (× 5); B, sketch of typical position of colony in water (× 3); C, flowering frond with characteristic broad base and lateral flower cavity (× 9); D, flowers in flower cavity with stigmatic droplet and showing pigmented line of dehiscence of anther (× 25); E, mature seed (× 25).

Wolffiella gladiata. F, typical shape and habit of growth (× 3.5); G, colony of plants in water (× 3.5). (Dotted lines indicate water level.)

H, distribution.

Wolffiella floridana



Wolffiella gladiata

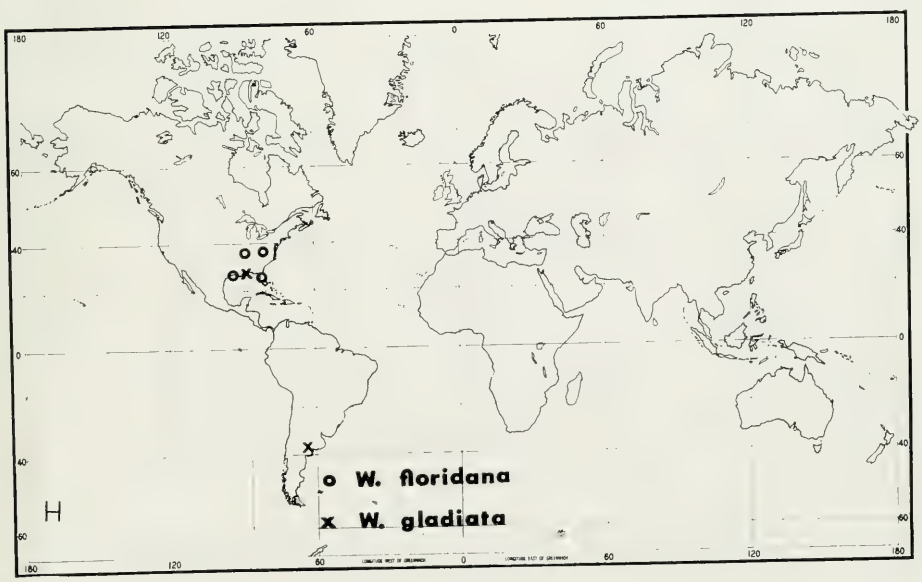


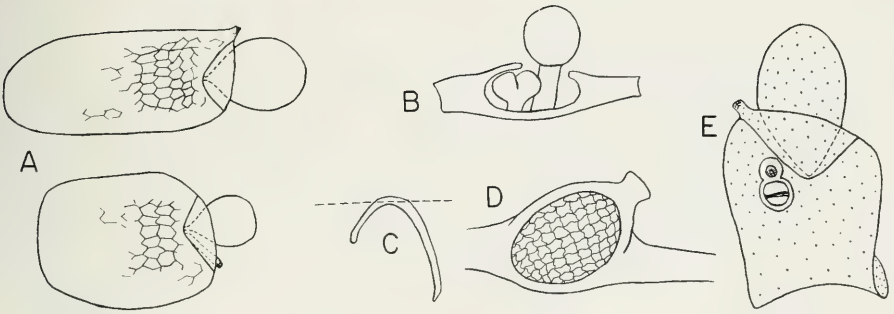
PLATE 15. *Wolffiella lingulata.*

A, typical adult fronds with air spaces in basal one-third only (× 3.5); B, flowering section of frond with flowers (× 10); C, position of parent and young frond in water (× 2); D, fruit with nearly ripe seed (× 22.5); E, flowering frond showing position of flower cavity and moderately punctate condition (× 5).

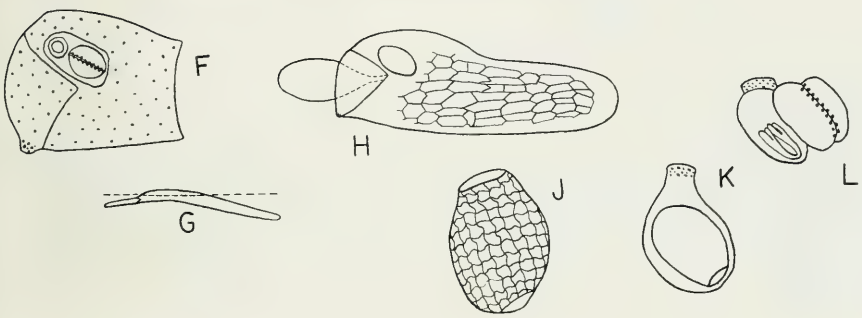
Wolffiella oblonga. F, basal section of flowering frond showing location of flowers and punctate cells (× 5); G, position of attached plants in water (× 2.5); H, adult frond with flower cavity and characteristic air spaces (× 5); J, mature seed showing striate seed coat (× 22.5); K, fruit with persistent punctate stigma (× 15); L, ovary and anther (× 25). (K, L, after Giardelli.)

M, distribution.

Wolffiella lingulata



Wolffiella oblonga



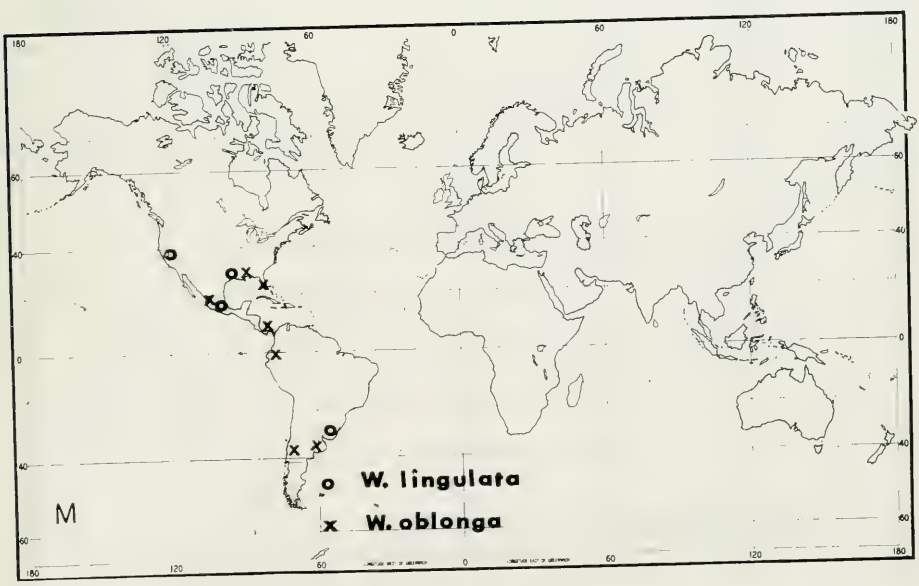
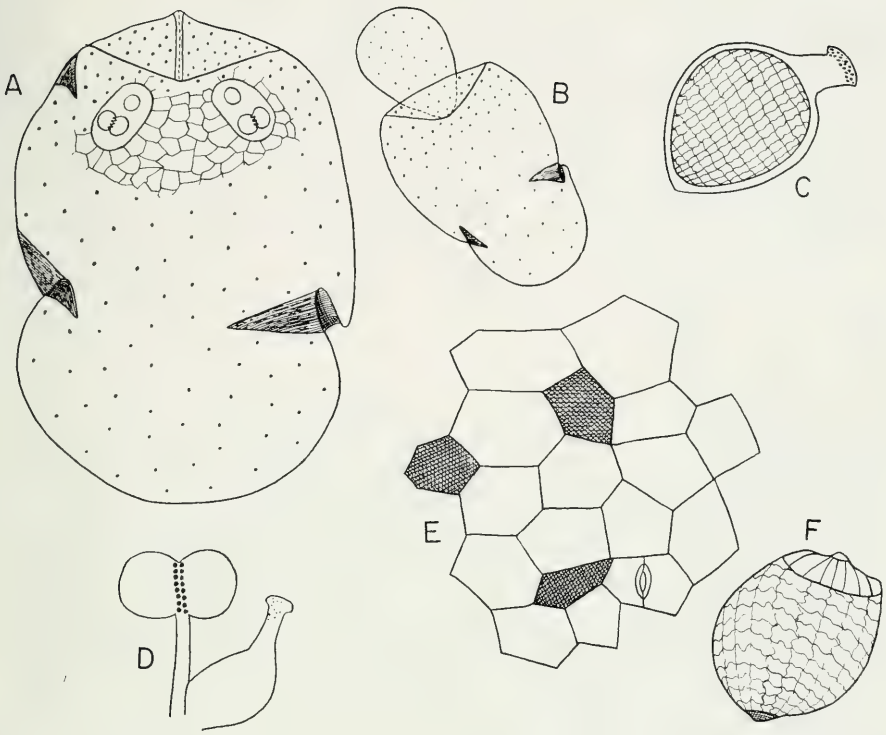


PLATE 16. *Wolffiella welwitschii.*

A, dorsal view of flowering plant showing two flower cavities, punctate cells, and curled margin (× 7.5); B, vegetative frond with young plant in reproductive pouch (× 3.5); C, fruit with persistent style and punctate stigma (× 25); D, ovary and anther (× 30); E, portion of upper epidermis showing pigment cells and stoma (× 120); F, mature seed with reticulate seed coat (× 30); G, distribution.

Wolffiella welwitschii



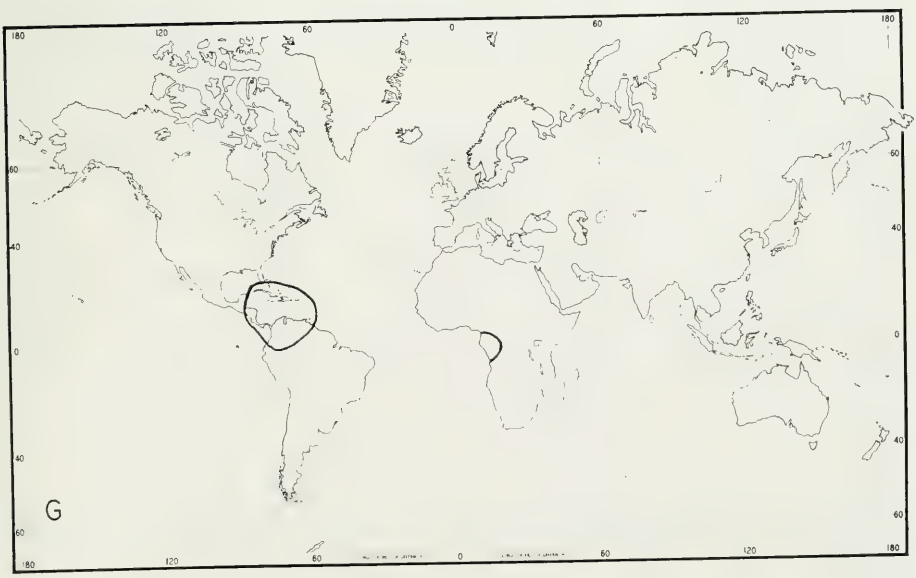


PLATE 17 (after Hegelmaier). *Wolffiella denticulata* (A-D).

A, adult frond (× 5); B, basal end of frond showing reproductive pouch, stipe, and young plant (× 17.5); C, denticulata apex and air spaces (× 15); D, lateral view of basal end showing elongated stipe (× 10).

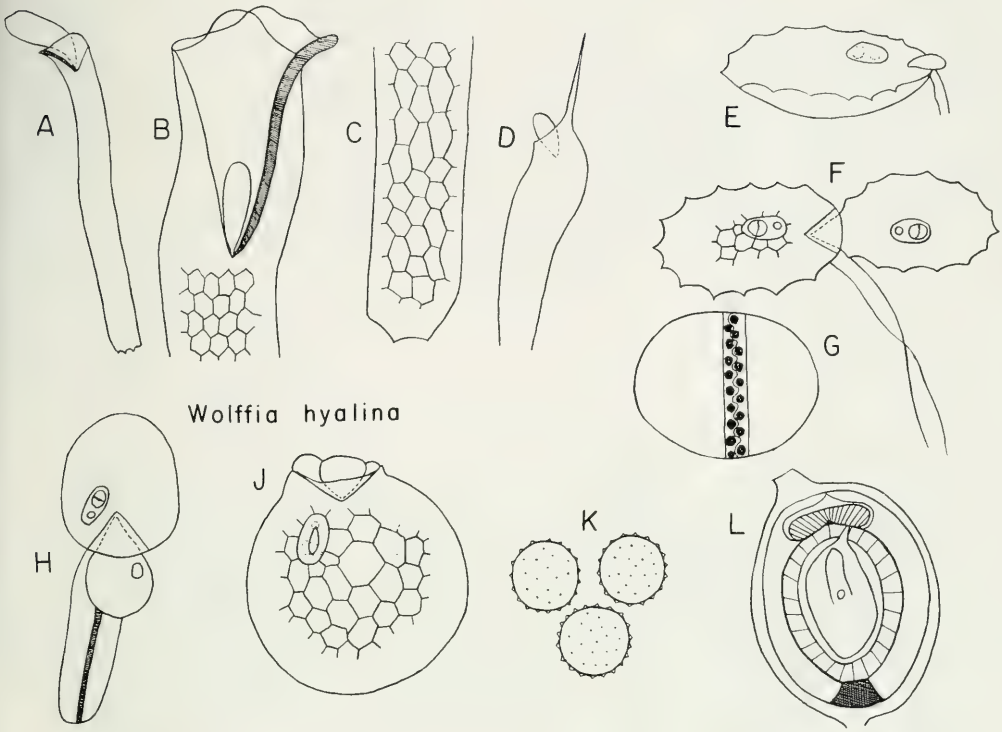
Wolffia repanda (E-G). E, lateral view of adult frond showing flat top and ovoid ventral surface (× 10); F, adult and young fronds, each flowering, from above, adult with elongated stipe (× 9); G, anther with pigmented line of dehiscence (× 60).

Wolffia hyalina (H-L). H, adult flowering frond with attenuate hyaline stipe (× 3.5); J, adult plant showing flared pouch, large air spaces, and flowering cavity (× 7.5); K, pollen grains, typical of all Lemnaceae (× 250); L, median section of fruit and seed with prominent operculum (× 37.5).

Distribution (M); *Wolffiella denticulata* (a); *Wolffia repanda* (b); *Wolffia hyalina* (c).

Wolffiella denticulata

Wolffia repanda



Wolffia hyalina

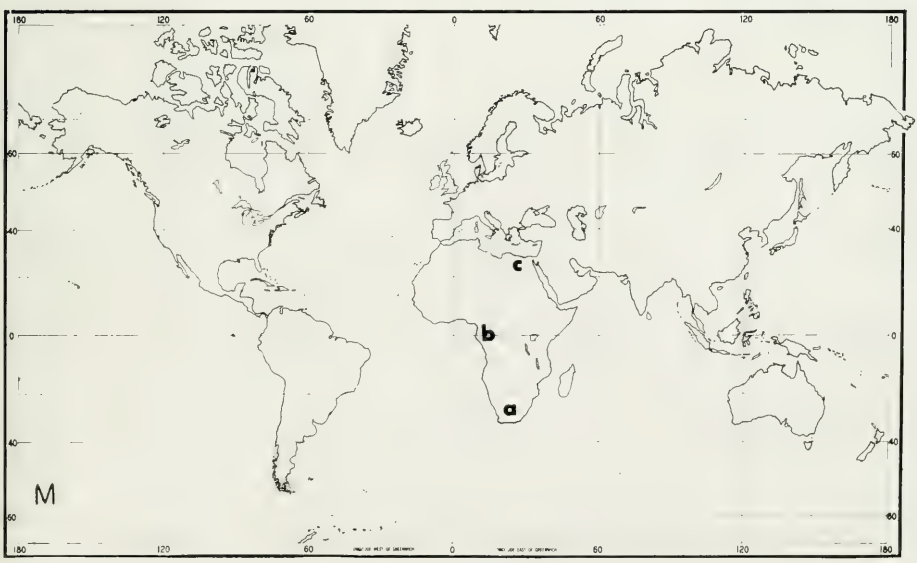


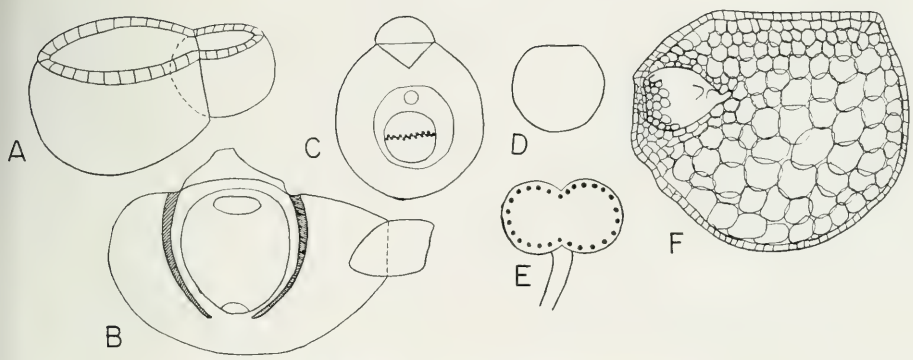
PLATE 18. *Wolffia arrhiza* (A-F).

A, adult frond showing flattened top and rounded margin or shoulders (× 25); B, median longitudinal section of fruiting plant with well-developed seed (× 40); C, dorsal view of flowering plant showing stigma and anthers (× 22.5); D, frond outline in median lateral section (× 12.5); E, opened anther (× 45); F, median longitudinal section of frond showing young plant, shape of outline, and arrangement of air spaces (× 37.5).

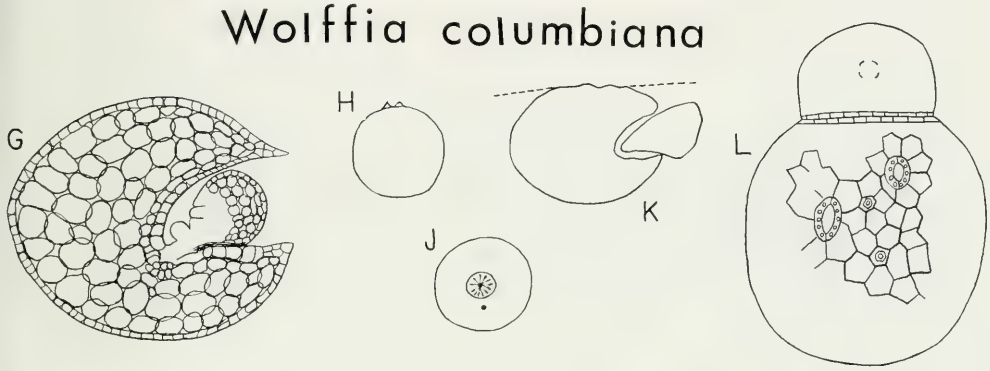
Wolffia columbiana (G-L). G, median longitudinal section showing outline and air space arrangement (× 22.5); H, outline in median transverse section (× 10); J, basal end showing funnel-shaped reproductive pouch and stipe (× 10); K, position in water, roughened surface only projecting (× 12.5); L, dorsal view showing stomata and large air spaces (× 22.5).

M, distribution.

Wolffia arrhiza



Wolffia columbiana



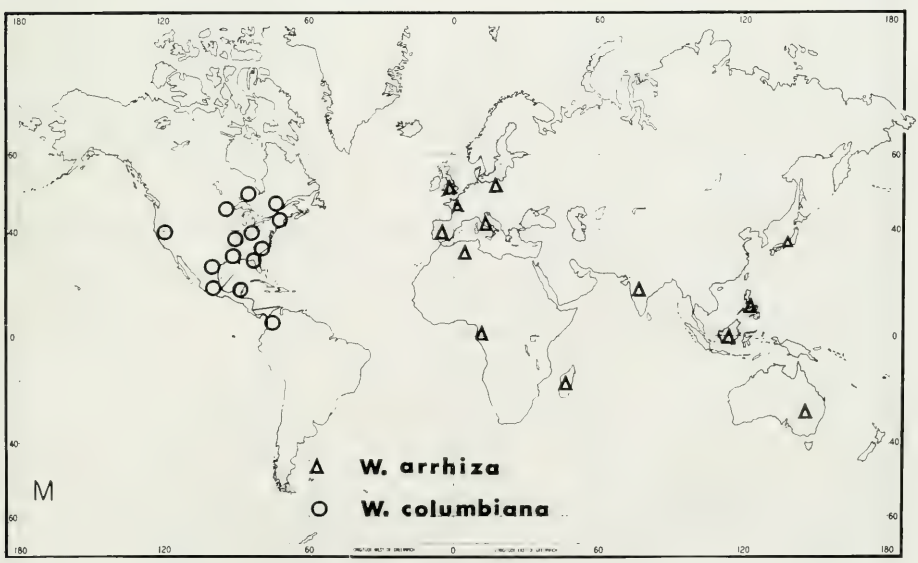


PLATE 19. *Wolffia papulifera.*

A, adult and young plants showing papules and punctate condition (× 15); B, dorsal view, showing minutely denticulate margin (× 12.5); C, median longitudinal section of flowering plant (× 37.5); D, fruiting plant with nearly mature seed (× 25); E, section of upper epidermis showing punctate cells and stomata (× 90); F, anther with punctate line of dehiscence (× 40); G, anther after shedding pollen (× 40); H, dorsal view of flowering plant (× 15); K, distribution.

Wolffia papulifera

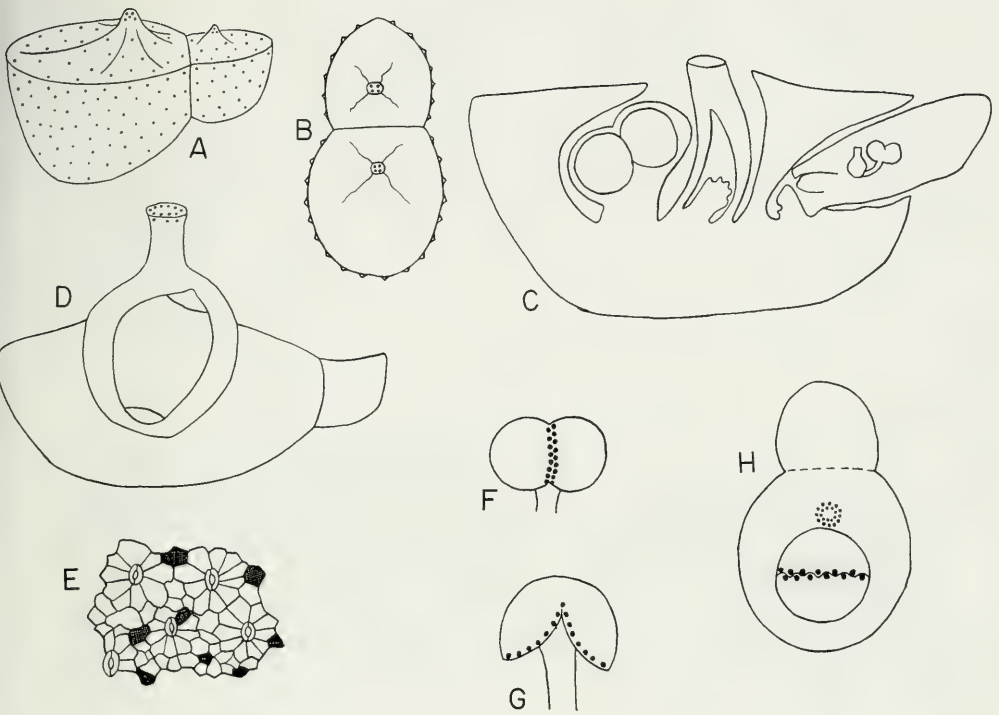


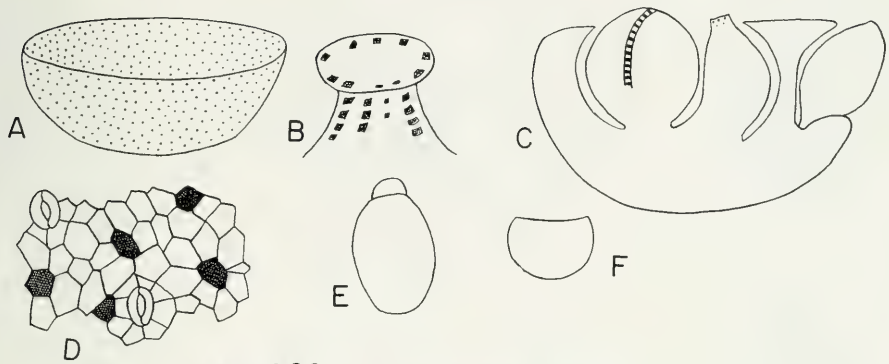
PLATE 20. *Wolffia brasiliensis* (A-F).

A, lateral view of adult plant (× 20); B, punctate style and stigma (× 150); C, nearly median long section of flowering plant with young plant in reproductive pouch (× 25); D, section of upper epidermis showing punctate cells and stomata (× 120); E, dorsal view outline (× 20); F, outline in median transverse section (× 10).

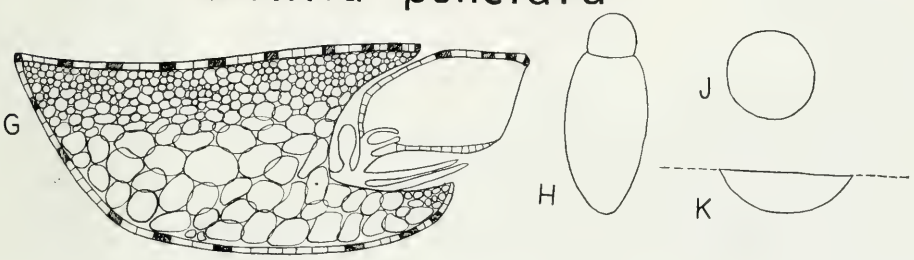
Wolffia punctata (G-K). G, median long section showing typical shape, punctate epidermal cells, arrangement of air spaces, and young plant attached (× 37.5); H, dorsal view outline (× 10); J, outline in median transverse section (× 10); K, position in water.

L, distribution.

Wolffia brasiliensis



Wolffia punctata



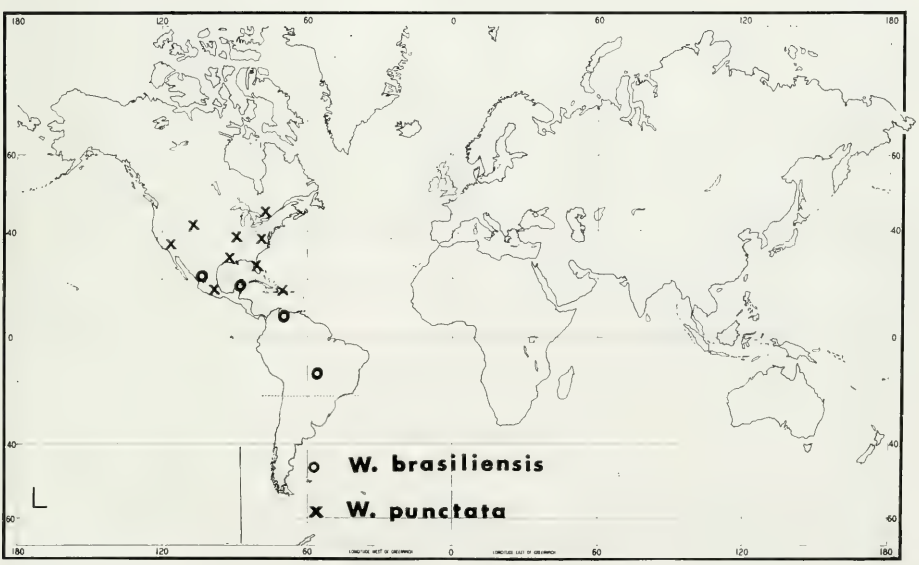
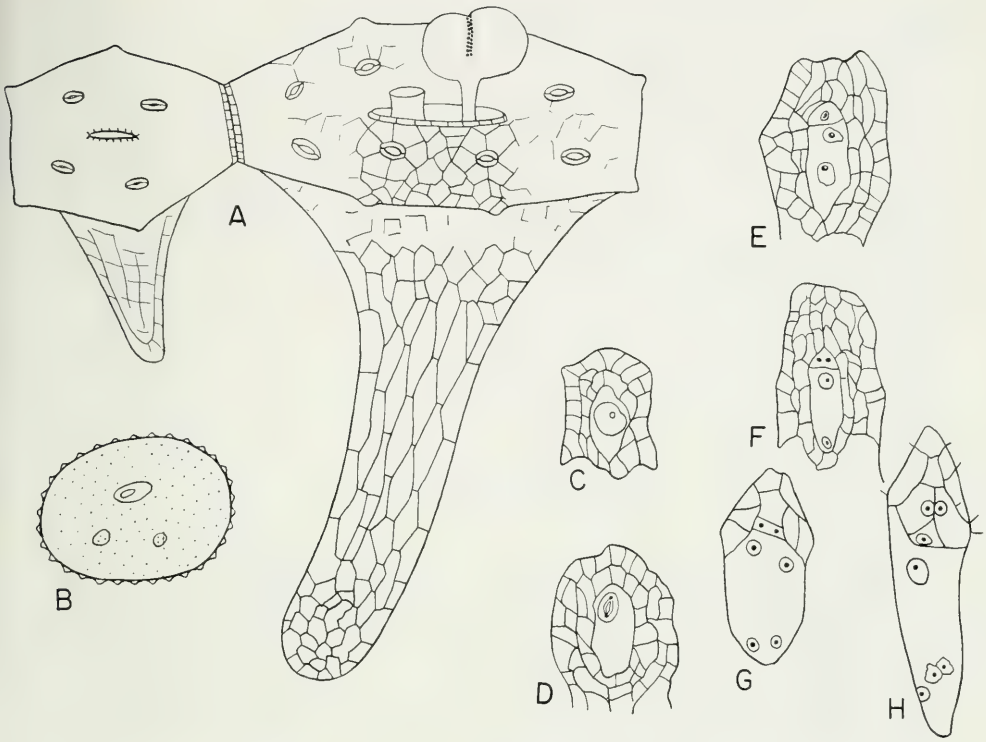
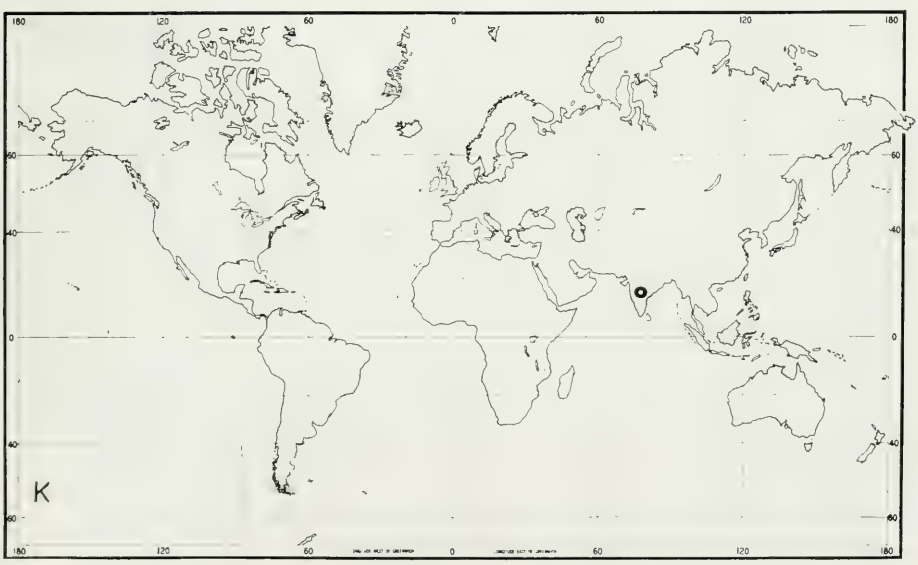


PLATE 21. *Wolffia microscopica.*

A, typical plant with attached young plant, showing characteristic shape, flowers, and dentate margin (× 45); B, three-nucleate pollen grain (× 750); C-H, successive stages in development of embryo sac (after Maheshwari); C, megaspore mother cell; D, telophase of meiosis I; E, two-nucleate embryo sac with degenerating upper dyad cell; F, same except nucleus of upper dyad cell has also divided; F, four-nucleate embryo sac; H, mature embryo sac, seven-nucleate as a result of fusion of the two polar nuclei before fertilization; K, distribution.

Wolffia microscopica





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VI. SIGNIFICANT COLLECTIONS (unnumbered)

Several important and widely distributed collections contain specimens which are not identified by number and thus cannot be listed herein with the numbered specimens. Some of the more noteworthy of these are acknowledged as follows. L. Hahn (before 1868: MO, F, US), his Mexican collections include the type specimens of *Wolffiella gladiata* and *W. lingulata*. C. F. Austin (responsible for the treatment of the Lemnaceae in the 5th edition of *Gray's Manual*, and authority for the varietal epithets of *Lemna minor* var. *trinervis* and *L. minor* var. *obscura*) has collections in MO, US, F. C. H. Thompson (authority for the binomial *Wolffia papulifera* and the combination *Wolffiella floridana*, and author of the only North American monograph of the family) has collections in US and MO. Dr. George Engelmann (MO) collected extensively near St. Louis, Missouri. His collections are cited by Hegelmaier and used by the latter as source material for many of his descriptions. Elihu Hall (ILL, MO) made many collections in central Illinois (these collections frequently cited by Hegelmaier). Henry Gillman (US, MO, F, UC) collected many species

in flower and fruit from near Detroit in 1870 and 1871. J. D. Smith (authority for the varietal epithet *floridana*) has collections in MO, F, US.

There are many other collectors, frequently well-known in the botanical world, whose collections of Lemnaceae are of interest though perhaps less significant than those mentioned above. These include Trelease (MO), Leggett (US, MO), E. J. Hill (ILL), John Torrey (US, MO), Eggert (ILL, MO, US), Ravenel (MO), and Umbach (ILL).

VII. LIST OF FLOWERING AND FRUITING SPECIMENS EXAMINED

Collector, number, and location of specimen:	Date and place of collection:	Flowering:	Fruiting:
	Spirodela intermedia (1)		
Burkhart 8521 (UC)	Nov. 20, 1937 (Arg.)	X	X
	Spirodela polyrhiza (2)		
Gillman (UC, MO)	July 30, 1871 (Mich.)	X	
Leggett (MO)	Aug. 1870 (N.Y.)	X	X
	Spirodela oligorhiza (4)		
Godfrey 60574 (FSU)	Mar. 3, 1961 (Fla.)	X	X
Godfrey 60601 (FSU)	Mar. 3, 1961 (Fla.)	X	
	Spirodela punctata (5)		
Wilkes Exp. (US, MO)	Feb.-Apr. 1839 (Arg.) (Terra del Fuego)	X	X
	Lemna gibba (6)		
B. Thompson (MO)	Aug. 12, 1896 (Cal.)	X	
C. H. Thompson (MO)	Oct. 19, 1902 (Cal.)	X	X
A. Nelson (MO)	July 25, 1901 (Wyo.)	X	
Engelmann (MO)	July 1868 (Mo.)	X	
Simmons (MO)	July 20, 1891 (Swed.)	X	
Henney 109 (MO)	Sept. 1896 (Cal.)	X	
Julio II–44 (US)	(Bol.)	X	
Julio II–196 (US)	1930 (Bol.)	X	
Smith & Nobs 1826 (UC)	Sept. 3, 1949 (Cal.)	X	
Giardelli 521 (UC)	Jan. 26, 1935 (Arg.)	X	X
Nobs & Smith 3 (UC)	July 6, 1948 (Cal.)	X	
Nobs & Smith 837 (UC)	June 23, 1949 (Cal.)	X	
Nobs & Smith 916 (UC)	June 30, 1949 (Cal.)	X	
Nobs & Smith 955 (UC)	July 11, 1949 (Cal.)	X	X
Nobs & Smith 956 (UC)	July 12, 1949 (Cal.)	X	X
Brandegee (UC)	(Cal.)	X	
A. Nelson (MICH)	Aug. 1912 (Wyo.)	X	
Heller & Brown 5571 (MICH)	May 19, 1902 (Ariz.)	X	
A. Braun (MO)	(Ger.)	X	X

Collector, number, and location of specimen:	Date and place of collection:	Flowering:	Fruiting:
	Lemna disperma (7)		
Giardelli 535 (UC)	Dec. 26, 1934 (Arg.)	X	X
	(Distributed as *L. parodiana*)		
	Lemna obscura (8)		
Godfrey 55745 (UC, FSU)	July 26, 1957 (Fla.)	X	X
Hitchcock 1 (F)	June 1898 (Fla.)	X	
	Lemna minor (9)		
Gillman (MO, UC)	July 30, 1871 (Mich.)	X	
Leggett (MO, F)	1885 (N.Y.)	X	X
——— (MO)	Aug. 14, 1868 (N.Y.)	X	X
Gillman (MO)	June 7, 1870 (Mich.)	X	
Eggert (MO)	1875 (Mo.)	X	
Garber (US)	Oct. 1872 (Pa.)	X	
Lindberg 143 (UC)	June 30, 1889 (Fin.)	X	
Ogden & Wiggins 1730 (UC)	Oct. 3, 1937 (Mass.)	X	X
Nobs & Smith 1051 (UC)	July 21, 1949 (Cal.)	X	
V. H. Chase 13137 (ILL)	Oct. 1952 (Ill.)		X
Eggert (UC)	Aug. 17, 1896 (Ill.)		X
Mackenzie (F, MO)	July 19, 1896 (Mich.)	X	X
Bush 524 (US)	July 1896 (Mo.)		X
Hegelmaier (MO)	June 1867 (Ger.)		X
Wilson (UC)	June 1897 (Ind.)	X	X
	Lemna perpusilla (10)		
Bush 584	Aug. 9, 1896 (Mo.)		X
Schneck (MO)	Sept. 1877 (Ill.)		X
Thompson (MO)	1896 (Mo.)		X
Eggert (MO)	Aug. 21, 1896 (Ark.)		X
Drouet *et al.* 3721 (MO)	Nov. 22, 1939 (Mex.)	X	X
Fassett 28543 (MO)	Jan. 1, 1951 (El Salv.)	X	X
Svenson 87 (MO)	Apr. 10, 1930 (Galap. Is.)		X
Eggert (US, UC)	Aug. 17, 1896 (Ill.)		X
Mackenzie (US)	Aug. 9, 1896 (Mo.)		X
Svenson 11024 (US)	Mar. 22, 1941 (Ecuad.)		X
Gould & Robbins 3607 (UC)	July 30, 1946 (Ariz.)	X	X
Thivy 131 (MICH)	Oct. 10, 1947 (India)		X
Small (F)	Sept. 21, 1889 (Pa.)	X	
Daubs 829 (ILL)	June 15, 1961 (Ark.)		X
Daubs 832 (ILL)	June 15, 1961 (Ark.)	X	X
Daubs 862 (ILL)	July 22, 1961 (Ill.)	X	X
Daubs 900 (ILL)	Feb. 8, 1962 (Fla.)		X
Palmer 177 (MICH)	Sept. 1897 (Mex.)		X
S. C. Maheshwari (ILL)	Sept. 1954 (India)	X	X
	Lemna trinervis (11)		
Hitchcock 373 (F)	July 1900 (Fla.)	X	X
Daubs 797 (ILL)	June 1, 1961 (Miss.)	X	X
Trelease 202/99 (MO)		X	X

Collector, number, and location of specimen:	Date and place of collection:	Flowering:	Fruiting:
	Lemna valdiviana (12)		
Austin (MO)	Sept. 1862 (N.J.)		X
Coursillons (MO)	Apr. 25, 1902		X
Reverchon (MO)	June 27, 1900 (Tex.)		X
Daubs 754 (ILL)	May 28, 1961 (Fla.)	X	X
	Lemna minima (13)		
Mason 11545 (UC)	June 17, 1937 (Cal.)	X	X
	Lemna trisulca (14)		
Moore & Huff 18647 (ILL)	June 1946 (Minn.)	X	
Gillman (MO)	July 30, 1871 (Mich.)	X	
Gillman (UC)	July 16, 1871 (Mich.)	X	
Gillman (UC)	Aug. 6, 1871 (Mich.)		X
Bernhardi Herb. (MO). No collector or date		X	X
Hegelmaier (MO)	May 31, 1863 (Ger.)	X	
Hahn (MO)	(Mex.)	X	
Fendler 1007 (MO)	Aug. 17, 1843 (N. Mex.)	X	X
	Wolffiella welwitschii (15)		
Wright 70 (MO)	Mar. 1869 (Cuba)	X	X
Britton & Nelson 268 (MO)	Sept. 4, 1903 (Cuba)	X	X
Det. by Hegelmaier (MO)	Nov. 1853 (Angola)	X	X
	Wolffiella lingulata (16)		
Daubs 616 (ILL)	Dec. 29, 1960 (Mex.)		X
Daubs 618 (ILL)	Dec. 30, 1960 (Mex.)		X
Carter 3453 (UC)	June 27, 1955 (Cal.)	X	
Mason 11850 (UC)	June 12, 1938 (Cal.)	X	
Mason 11548 (UC)	June 21, 1937 (Cal.)	X	
Mason & Smith 8227 (UC)	July 28, 1948 (Cal.)	X	
	Wolffiella floridana (18)		
Daubs 758 (ILL)	May 29, 1961 (Fla.)	X	X
Daubs 664 (ILL)	Feb. 3, 1961 (Fla.)	X	X
(Daubs 664 flowered and fruited in the laboratory)			
	Wolffiella oblonga (20)		
Lorentz & Hieronymus 554 (MO)	June 28, 1873 (Arg.)	X	
	Wolffia hyalina (22)		
Sickenberger (UC)	Nov. 13, 1890 (Egypt)	X	X
	Wolffia microscopica (23)		
S. C. Maheshwari (ILL)	Nov. 10, 1952 (India)	X	X
	Wolffia brasiliensis (24)		
Lasser 2004 (MICH)	July 1946 (Venez.)		X
Steere 1567 (MICH)	June 25, 1932 (Mex.)	X	X
	Wolffia papulifera (26)		
Peterson 3115 (MO, US)	Jan. 9, 1955 (Arg.)	X	X
Hubricht B696 (MO)	Nov. 6, 1937 (Ill.)	X	X
	Wolffia columbiana (27)		
Rogers (ILL)	Aug. 1932 (Iowa)	X	X

Collector, number, and location of specimen:	Date and place of collection:	Flowering:	Fruiting:
	Wolffia arrhiza (28)		
R. N. Parker (UC)	Nov. 10, 1927 (India)	X	X
Thivy 139 (MICH)	Jan. 15, 1948 (India)	X	X
Suekele (?) 4428	Feb. 23, 1919 (Malay)	X	X

VIII. SUMMARY

The aquatic plant family Lemnaceae is represented in the world by 28 species and one variety. These taxa are separated into four genera: *Spirodela* (5 spp. and one var.), *Lemna* (9 spp.), *Wolffiella* (6 spp.), and *Wolffia* (8 spp.). The family is related to Araceae through the water-lettuce *Pistia stratiotes* L.

The Lemnaceae are of temperate and tropical distribution and some species are found in these zones throughout the world, even though some species are of distinctly limited distribution. *Spirodela oligorhiza,* formerly regarded as a Far Eastern species, is now found to be widely distributed in the United States. *Lemna gibba* is also found to occur, perhaps sporadically, in the eastern United States. *Spirodela polyrhiza* and *Lemna trisulca* are apparently absent from South America. *Lemna minor* is the most cosmopolitan, being found from South Africa to Alaska. *Lemna trisulca* is only infrequently found in the warmer areas. The genus *Wolffiella* is limited almost exclusively to the Western Hemisphere.

This family represents within its individual members the ultimate in reduction in size and complexity and in the genus *Wolffia* has the world's smallest flowering plants. Vascular tissue is almost always completely lacking in *Wolffia* and *Wolffiella.* The reduction series is interpreted as a regressive one with *Spirodela,* the most complex in structure, as primitive, and *Wolffia* as the most advanced.

Some of the more significant findings of this study are as follows:

(1) Neither the flowering nor fruiting structures are of much significance in delimiting species, but are often of value in delimiting genera.

(2) The validity of determining species primarily on the basis of vegetative structures is examined and accepted.

(3) *Lemna trinervis* (Austin) Small is reappraised and Small's combination is accepted.

(4) *Lemna paucicostata* and *Lemna aequinoctialis* are placed in synonymy with *Lemna perpusilla.*

(5) *Lemna parodiana* is placed in synonymy with *Lemna disperma.*

(6) *Lemna obscura* (Austin) comb. nov. is proposed to replace *Lemna minor* var. *obscura* (Austin).

(7) *Wolffiella welwitschii* is proposed to replace *Wolffia welwitschii.*

(8) *Spirodela polyrhiza* var. *masonii* var. nov. is proposed for a new variety described from the Netherlands.

(9) The relationship of *Lemna minima* to *Lemna valdiviana* is discussed and both species are accepted.

(10) Both the gibbous and nongibbous forms of *Lemna gibba* are included in the one species, and the conditions under which gibbosity occurs are proposed for further investigation.

(11) *Wolffia cylindracea* is placed in synonymy with *Wolffia arrhiza.*

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FULL TITLES OF SERIAL ABBREVIATIONS

Acta bot. fennica
Acta botanica fennica. Helsingfors.

Acta bot., Zagreb
Acta botanica. Botanicki Zavod. Zagreb University.

Acta Soc. Bot. Polon.
Acta Societatis Botanicorum Poloniae. Warszawa.

Actes Soc. linn. Bordeaux
Actes de la Société linnéenne de Bordeaux.

Amer. Jour. Bot.
American Journal of Botany.

Amer. Mid. Nat.
The American Midland Naturalist.

Anal. Inst. Biol. Univ. Méx.
Anales del Instituto de Biología. Universidad Nacional, Mexico.

Ann. Bot.
Annals of Botany. London.

Ann. Sci. nat. III.
Annales de sciences naturelles. Troisième serie. Botanique.

Arch. de Botanique.
Archives de botanique. Caen.

Beiträge Pfl. Russ. Reich.
Beiträge zur Pflanzenkunde des Russischen Reiches.

Ber. schweiz. bot. Ges.
Berichte der schweizerischen botanischen Gesellschaft.

Bot. Gaz.
The Botanical Gazette.

Bot. Jb. (Engler)
Engler's Botanische Jahrbucher für Systematik, Pflanzengeschichte und Pflanzengeographie.

Bot. Notiser
Botaniska Notiser.

Bot. Rev.
Botanical Review. London.

Bot. Tidsskr.
Botanisk Tidsskrift.

Bot. Zeit.
Botanische Zeitung.

Bull. mens. Soc. linn. Paris.
Bulletin mensuel Société linnéenne de Paris.

Bull. Soc. Bot. Belg.
Bulletin de la Société Royale de botanique de Belgique.

Bull. Torrey bot. Cl.
Bulletin of the Torrey Botanical Club.

Canad. Fld Nat.
Canadian Field Naturalist.

Canad. Jour. Res. C.
Canadian Journal of Research. D; Botanical Sciences.

Chron. bot.
Chronica botanica.

Curr. Sci.
Current Science.

Ecol. Monogr.
Ecological Monographs.

Jour. agr. Res.
Journal of Agricultural Research.

Jour. Bombay Nat. Hist. Soc.
Bombay Natural History Society Journal.

Jour. Bot.
The Journal of Botany, British and Foreign.

Jour. gen. Physiol.
Journal of General Physiology.

Jour. Ind. Bot.
Journal of Indian Botany. (Indian Botanical Society Journal.) Madras.

Jour. Linn. Soc. London
Journal of the Linnean Society (of London). Botany.

Jour. Phys. Chim. Hist. nat.
Journal de physique, de chimie et d'histoire naturelle élémentaires. Paris.

Nederl. kruidk. Arch.
Nederlandsch kruidkundig archief. Leyden.

New Phytol.
New Phytologist; a British Botanical Journal.

Notas Mus. La Plata
Notas del Museo de La Plata.

Nova Acta Acad. Leop. Carol. Deut. Akad. Naturw.
Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae naturae curiosorum. Deutschland Akademie fur Naturwissenschaften.

Ohio Jour. Sci.
Ohio Journal of Science.

Physiol. and Ecol. Contr. Otsu Hydrobiol. Expt. Sta. Kyoto Univ.
Physiological and Ecological Contributions of Otsu Hydrobiological Experiment Station. Kyoto University.

Plant Physiol.
Plant Physiology.

Proc. Iowa Acad. Sci.
Proceedings of Iowa Academy of Science.

Proc. Linn. Soc. B.
Journal of Proceedings of Linnean Society of London. Botany.

Proc. Royal Soc.
Proceedings of the Royal Botanical Society of London.

Proc. Univ. Durham Phil. Soc.
Proceedings of Philosophical Society of Durham University.

Quart. Jour. Fla. Acad.
Quarterly Journal of the Florida Academy of Science.

Rep. Mo. Bot. Gard.
Missouri Botanical Garden. Annual Report.

Rev. argent. Agron.
Revista argentina de agronomia.

Rev. sudam. Bot.
Revista sudamericana de botanica.

Soil Sci.
Soil Science.

Trans. and Proc. N. Z. Inst.
Transactions and Proceedings Royal Society of New Zealand. Wellington.
Verh. siebenb. Ver. Naturw.
Siebenburgischer Verein für Naturwissenschaften. Verhandlungen und Mitteilungen.
Z. Naturw.
Zeitschrift für Naturwissenschaften.

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